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EVALUATION OF MASS SELECTION FOR GRAIN YIELD AND ESTIMATION OF GENETIC VARIABILITY IN THREE SELECTED MAIZE (ZEA MAYS L.) POPULATIONS

Iowa State University PH.D. 1981

Evaluation of mass selection for grain yield and estimation of genetic variability in three selected maize (*Zea mays* L.) populations

by

Mulamba Ngandu-Nyindu

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INTRODUCTION

The ultimate goal of most maize (Zea mays L.) breeding programs is the improvement of grain yield. The important contribution of the United States to the total world maize production and the success of maize production in the U.S. Corn Belt and other maize growing areas have been attributed to extensive use of adapted hybrids and improved field husbandry (Russell, 1974). Although there is general interest among maize breeders to broaden the germplasm base of maize breeding programs, recent surveys indicate that very few inbred lines are extensively used in commercial hybrid production (Zuber, 1975). Many of the widely used inbred lines also either have a common genetic background or have evolved from pedigree or backcross selection programs involving the commonly used lines. Several studies have shown, however, that recurrent selection procedures are powerful selection methods for the improvement of broad genetic base populations and for adapting exotic germplasm. Recurrent selection also provides the opportunity of extracting superior inbred lines with high performance in hybrid combinations from the improved populations.

Mass selection is the simplest, the most economical, and the most expedient method of recurrent selection. The effectiveness of mass selection, however, seemed to be limited to highly heritable characters. Refinement of the plot and

selection techniques for mass selection by Gardner (1961) renewed breeders' interest in mass selection for the improvement of complex characters, such as grain yield.

Mass selection for grain yield was initiated in the 'Krug (BSK)' variety in 1961. Hallauer and Sears (1969) reported the preliminary results after six cycles and observed very limited progress. Mass selection for grain yield in Krug continued and 14 cycles have been completed. Before mass selection was initiated, two recurrent selection programs were initiated in the Krug variety in 1952; one was based on S_1 progeny performance per se and the second on testcross (half-sib family) performance. Eight cycles of selection have been completed for each of these two recurrent selection procedures.

Objectives of my study were to: (1) evaluate the effectiveness of mass selection for grain yield improvement after 14 cycles of selection, (2) determine the correlated response in other plant traits, (3) compare the relative effectiveness of the three selection procedures for the improvement of Krug (BSK) for yield and other agronomic traits based on S_1 progenies, and (4) determine the effect of the three selection procedures on the genetic variation within the three selected Krug populations.

LITERATURE REVIEW

Recurrent Selection

Recurrent selection is directed toward the improvement of the population by increasing the frequency of favorable alleles for a given trait in a desired direction. Recurrent selection involves repeated cycles of selection and recombination to constitute new populations from selected genotypes. This breeding system has been extensively used for improving important agronomic traits of various crops, particularly maize (Zea mays L.)

Penny et al. (1963) classified recurrent selection procedures based on either a phenotypic or genotypic evaluation. Phenotypic recurrent selection, or mass selection, included those instances where S_0 plants are the bases of selection, whereas genotypic recurrent selection included all types of selection in which the merit of S_0 plants was determined on the basis of the average performance of their progeny (family selection). From their viewpoint, five types of recurrent selection were recognized: (1) phenotypic (mass) recurrent selection, (2) recurrent selection based on S_1 or S_2 progeny performance, (3) recurrent selection based on half-sib family, (4) recurrent selection based on full-sib family, and (5) reciprocal recurrent selection. Further subdivision was considered for testcrosses or half-sibs on the basis of homozygosity or heterozygosity of the tester involved. Another type

of recurrent selection would be the combination of two or more selection methods in the same breeding program as outlined by Goulas and Lonnquist (1976). Moll and Stuber (1974) classified recurrent selection into two broad categories: (1) intrapopulation improvement and (2) interpopulation improvement. Intrapopulation schemes maximize improvement of populations per se and their derived inbred lines. Interpopulation schemes maximize improvement of population crosses and hybrids between lines derived from the populations under selection.

Hayes and Garber (1919) developed recurrent selection schemes to improve the protein content of the open-pollinated variety, 'Minnesota 3'. A number of plants were self-pollinated and ears with high-protein content were selected based on chemical analysis. The selected strains were intermated and the resulting progenies were planted in isolation blocks and selected for vigor. Comparisons of the original and improved populations showed that the improved populations had higher percentage of protein and yield. East and Jones (1920) also used a similar selection scheme to develop a high-protein strain of maize.

Jenkins (1940) outlined a breeding procedure to develop more productive synthetic varieties from short-term inbred lines. Based on the assumption that heterosis was due to dominance effects of desirable genes, plants were selfed and crossed to a heterozygous tester with a broad genetic base, which was the parental variety. This method was subsequently

described as recurrent selection for general combining ability because it used a broad genetic base tester. Jenkins' proposal included the following phases: (1) isolation of selfed lines in one generation, (2) testing of lines in testcrosses for yield and (or) other desirable traits, (3) selecting and intercrossing the best lines to produce a synthetic variety, and (4) repeating the above steps for each subsequent synthetic after one or two generations of recombination. The phases described by Jenkins (1940) are similar to those included for other methods of recurrent selection.

Hull (1945) was the first to use the term "recurrent selection". He described a breeding scheme similar to that described by Jenkins (1940); the only modification was the use of a narrow genetic base tester (a homozygous line) as the tester. Hull (1945) calculated that yield of F_1 hybrids exceeded the sum of their respective inbred parents by more than 20%, and he suggested that overdominance was the major cause of yield heterosis. Hence, Hull (1945) proposed that selection should be emphasized for loci that exhibited overdominant effects. Hull's proposal was termed recurrent selection for specific combining ability.

Sprague and Eberhart (1977) summarized the different recurrent selection studies conducted in different maize populations for grain yield improvement. Average genetic gain was about 3 to 5% per cycle for the different methods of recurrent selection. Gain per cycle was similar to those reported by

Darrah et al. (1978) for different recurrent selection methods initiated in three maize populations at Kitale, Kenya, except for reciprocal recurrent selection. Greater genetic gain per cycle (7%) was observed for reciprocal recurrent selection in Kenya as compared to 3.5% obtained in the North Carolina and 4.5% obtained in the Iowa selection programs. Hence, in most instances, recurrent selection has been effective in improving maize yield regardless of the method used.

Mass Selection

Phenotypic recurrent selection, or mass selection, is the oldest breeding method used for maize improvement. The effectiveness of mass selection, however, has been limited primarily to qualitative traits and highly heritable traits; e.g., prolificacy (Kincer and Josephson, 1976; Lonnquist, 1967), ear length (Hallauer, 1968; Cortez-Mendoza and Hallauer, 1979), ear height (Acosta and Crane, 1972), early silking (Hallauer and Sears, 1972; Troyer and Brown, 1972), insect resistance (Zuber et al., 1971), and some other plant and ear characters. For traits such as grain yield that have a relatively low heritability, mass selection resulted in very limited progress. Some maize breeders implicated the paucity of additive genetic variability as the major cause of the failure to improve maize grain yield with mass selection.

Mass selection for grain yield proved to be effective after the modifications introduced by Gardner (1961). By use

of the grid system and timely irrigation to minimize the environmental effects, Gardner estimated the average gain for the first four cycles of selection for grain yield improvement to be 3.9% per cycle in the 'Hays Golden' variety. After six cycles, Lonnquist et al. (1966) reported 2.1% of gain per cycle. Gardner (1969, 1973) reported a gain of 3% per cycle after 15 generations. After the 15th cycle, a yield reduction was observed, and it was hypothesized that genotype-environment interaction had caused a lack of response in later cycles of selection (Gardner, 1977, 1978; Mareck and Gardner, 1979).

Johnson (1963) obtained a gain in grain yield of 11% per cycle in a tropical variety after three cycles of selection. Eberhart et al. (1967) reported an increase in yield of 7.42% in 'Kitale Composite Syn 3' after one cycle of mass selection. Ten cycles later, Darrah et al. (1978) observed a gain of 1.13% per cycle. Hakim et al. (1969) obtained a 9% yield improvement in the first cycle of mass selection when the selected population was tested in the same season and an average of 4% over environments.

Hallauer and Wright (1967) reported a gain of 1.5% after three cycles of mass selection in the 'Iowa Ideal' maize variety. The increase in yield was accompanied by increased moisture, root lodging, and dropped ears. Two additional cycles in the same population reported by Hallauer and Sears (1969) showed a nonsignificant yield increase. Hallauer and Sears (1969) also reported no significant yield improvement in

the Krug maize variety, which had undergone six cycles of mass selection for grain yield. They hypothesized that the lack of significant response may be due to one or more of the following factors: (1) paucity of additive genetic variance, (2) imprecise plot techniques to minimize the confounding effects of the environment, (3) insufficient testing to detect the small differences among the different cycles of selection, (4) a lower intensity of selection because of the exclusion of stalk-lodged plants in the basic units of selection, and (5) plant density was too high to permit the phenotypic expression of yield for individual plant genotypes that could be selected visually.

Mass selection for other plant and ear traits have increased grain yield. Results of five cycles of selection for prolificacy in the Hays Golden variety showed that increased number of ears per plant improved grain yield at the rate of 6.28% per cycle (Lonnquist, 1967). Torregroza and Harpstead (1967) compared the effectiveness of divergent mass selection for single and multiple ears initiated in a Columbian highland maize variety. Selection for prolificacy produced 28% more ears and increased grain yield 14%. Selection for single-eared plants reduced the number of ears per plant 7% and decreased yield 5% as compared to the original variety.

Arboleda-Rivera and Compton (1974) developed three subpopulations of maize via mass selection for prolificacy and grain yield for three different seasonal conditions (rainy

seasons, dry seasons, and both rainy and dry seasons). Grain yield and prolificacy of the rainy season selections increased 10.5% and 8.8% per cycle, respectively, when tested under the conditions similar to those of selection. The same population tested under dry seasons produced only 0.8 and 1.0% of gain per cycle for yield and prolificacy, respectively. Dry season selection increased grain yield by 2.5% per cycle under dry conditions and 7.6% per cycle under rainy seasons. The number of ears per plant increased 4.4% under dry and 11.4% under rainy season conditions. Selection under both seasonal conditions produced a gain in grain yield of 5.3% and 1.1% per cycle when tested under rainy and dry conditions, respectively. Similarly, the respective gains for ears per plant were 7.0 and 3.3% per cycle.

Kincer and Josephson (1976) reported a 13.2% increase in total number of ears in their mass selection program for prolificacy in the 'Jellicorse' maize variety. Indirect response in grain yield was small but similar to that from direct selection for grain yield. Genter (1976) used mass selection as a means of incorporating desirable traits (reduced ear and plant height; and decreased silking date, pollen-shed-to-silking interval, grain moisture, smutted plants, root and stalk lodging) from 25 Mexican races of maize into a single population. After 10 cycles, he reported a 171% increase in grain yield.

Cortez-Mendoza and Hallauer (1979) evaluated 10 cycles of

divergent mass selection for ear length in the 'Iowa Long Ear' synthetic variety. They obtained asymmetrical response for ear length and observed that selection for shorter ears was accompanied by correlated response for decreased grain yield per plant. Selection for increased ear length, however, resulted in nonsignificant change in grain yield. Similar results were reported by Lantin (1980) after evaluation of 10 cycles of mass selection for prolificacy in two synthetic varieties (BS10 and BS11). Although significant response for increased number of ears was obtained, no correlated response for grain yield was observed in either synthetic variety.

Half-sib Selection

Population improvement based on topcrossing to a tester is termed "topcross progeny test", "half-sib progeny test", or "half-sib family selection" (Sprague, 1966). Half-sib selection is also known as recurrent selection for combining ability. Depending on the type of tester involved, recurrent selection is for either specific combining ability based on testcrosses using a narrow genetic base tester (e.g., inbred or hybrid) or general combining ability based on testcrosses using a broad genetic base tester (e.g., open-pollinated, synthetic, or composite varieties). The ear-to-row system that uses the parental variety as tester is also considered as a type of half-sib selection.

Although the ear-to-row method has been used since 1896,

it was considered an ineffective method for improvement of maize grain yield. The lack of appropriate field plot techniques, inbreeding due to small populations, and lack of isolation caused the method to be neglected as a method for population improvement. After the modifications introduced by Lonnquist (1964), the ear-to-row method of selection was reconsidered as a powerful method for improving maize grain yield and other traits.

Paterniani (1967) applied modified ear-to-row selection to a Brazilian maize variety. After three cycles of selection, Paterniani reported a gain of 13.6% per cycle. Webel and Lonnquist (1967) conducted four cycles of modified ear-to-row selection in the open-pollinated variety Hays Golden and reported a gain of 9.44% per cycle. After 10 cycles of selection in the same population, Compton and Bahadur (1977) observed a gain of 5.26% per cycle. Results reported by Eberhart et al. (1967) also indicated that ear-to-row (selection only among families) is an effective method for the improvement of maize populations. After two cycles of selection, the gains per cycle were 2.8% and 11.4% for 'Kitale II' and 'Ecuador 573' populations, respectively. However, no gain was observed in the 'Kitale Composite A' population. After six years of selection, Darrah et al. (1978) observed 0.83 and 2.59 q/ha increase in yield per year in the Kitale II and Ecuador 573 populations, whereas H611 population showed a decrease in yield of -0.43 q/ha per year.

Lonnquist (1949) topcrossed 36 selected S_1 lines to the parental stock 'Krug Yellow Dent' to develop half-sib families that were tested in replicated trials. On the basis of the topcrosses performance, remnant S_1 seeds of the best eight topcrosses were recombined to form a high-yield synthetic. Seven other S_1 lines whose topcrosses performed poorly were used to synthesize a low-yield synthetic. The two populations were separately intermated in isolation and advanced to the third generation of recombination, which was referred to as the syn. 3 generation. Yield trials involving the high-yield and low-yield populations and their parental variety were conducted in two seasons. Results indicated that the low-yield syn. 2 population yielded 85 and 88% of the parental population whereas the high-yield syn. 2 population produced 142 and 118% of the original variety. The trials that included the syn. 3 generations showed that the syn. 3 generations (low and high) yielded more than their respective syn. 2 generations and the high-yield syn. 3 generation yielded 27% more than the original stock; the low-yield syn. 3 generation equalled the parental population. Lonnquist (1967) concluded that the results showed the effectiveness of topcross progeny test for evaluating combining ability of lines to be used in synthetic varieties.

Lonnquist and McGill (1956) applied similar selection methods to five maize populations: three open-pollinated varieties (Krug, Reid, and Dawes 2) and two synthetic

varieties (Synthetics A and B) derived from synthesis of 9 and 25 inbred lines, respectively. After one cycle of recurrent selection, they observed increases in yield of 22, 9, and 9% for Krug, Reid, and Dawes 2 populations, respectively. After two cycles of selection, the relative performance of Krug, Reid, Synthetic A,and Synthetic B populations were 98, 95, 102, and 88% of the commercial double-cross hybrid, US13, included as a check entry. In comparison, the same populations yielded 87, 86, 85, and 72% of US13 hybrid, respectively, after the first cycle of selection.

Lonnquist and Rumbaugh (1958) compared the relative importance of selection for specific and for general combining ability in the Krug maize variety. They selected 152 S_0 plants that were testcrossed with the single-cross, WF9 x M14. The best 31 testcrosses were selfed and then recombined to produce Synthetic KII. Similarly, 121 testcrosses were obtained by crossing 91 S_0 plants and 31 S_1 lines to the parental Krug variety. The 16 high yielding testcrosses were selected and their S_1 remnant seeds were intermated to form another synthetic, KIIs. The two synthetics were yield tested and results showed that KIIs and KII produced 98.5 and 95% of the check hybrid, US13, respectively. They concluded that selection based on broad-genetic base tester (i.e., general combining ability) was more effective than selection based on narrow-genetic base tester. Different conclusions, however, were obtained by Horner et al. (1963) who also compared the

relative effectiveness of an inbred-line tester (narrow-genetic base) and a genetically heterogeneous tester (broad-genetic base) with regard to combining ability for grain yield in the 'Florida 767' maize population. The population itself and the inbred line, F6, were used as testers. Evaluation of the first three cycles indicated that more progress was made with the narrow-genetic base tester than with the broad-genetic base tester. They concluded that a heterogeneous tester probably has several alleles at each locus that cause greater genetic variation within testcrosses, resulting in less effective selection.

Preliminary results from two cycles of recurrent selection for specific combining ability in the Krug population (using the single-cross hybrid WF9xM14 as tester) were reported by Lonnquist (1961). Grain yield increased at the rate of 3.4% per cycle. Penny et al. (1962) obtained gains of 7.2% and 1.1% for 'Alph' and 'WF9xB7' populations, respectively, after two cycles of selection for combining ability with the inbred tester, B14. Evaluation of the same program by Russell et al. (1973) after five cycles of selection showed the rates of gain per cycle to be 3.09% for Alph C_nxB14 and 1.32% for (WF9xB7)C_nxB14. Horner et al. (1976) evaluated progress after seven cycles of recurrent selection for specific combining ability with the single-cross hybrid, F44xF6, and the unrelated broad-genetic base synthetic, FS3W. Seven cycles of selection increased grain yield 18% (or 2.57% per

cycle), reduced ear height 9%, and reduced lodging 35% relative to the parental population. Similar performance was observed when the unrelated synthetic was used as tester. They concluded that the observed gains for these traits resulted from increased gene frequencies of alleles with additive effects.

Eberhart et al. (1973) evaluated changes in the 'Iowa Stiff Stalk Synthetic' after seven cycles of selection for combining ability with the double-cross hybrid, Ia13, as tester. Rate of gain for population per se was 1.4% per cycle while that for testcross selection was 2.6% per cycle.

Walejko and Russell (1977) evaluated five cycles of recurrent selection for combining ability in two open-pollinated maize varieties, 'Kolkmeier' and 'Lancaster', using Hy inbred line and the reciprocal population as testers. The populations per se displayed divergent results: a small but nonsignificant yield increase in the Kolkmeier variety and a significant, but negative change, in the Lancaster variety. Testcrosses with the inbred line, Hy, and the population crosses, however, showed linear and significant responses to selection over cycles. These results corroborated those reported by Eberhart et al. (1973) and Horner et al. (1973, 1976) and indicated the effectiveness of a narrow-genetic base tester in a recurrent selection program for improving grain yield.

S_1 Progeny Selection

Davis (1934) was the first to use S_1 progeny testing in maize, and he reported a correlation of 0.64 between yield of first- and second-generation maize inbreds and their topcross yields. Early generation testing also was proposed by Jenkins (1935) and included evaluation of S_0 plants via topcrossing. Topcrossing became widely accepted in maize breeding programs, and S_1 progeny testing received limited attention.

Sprague (1946) indicated that line performance in topcrosses remained relatively stable after the S_1 generation and suggested that additional selfing was unnecessary in the development of synthetic varieties. On the other hand, Lonnquist (1949) showed that general combining ability (i.e., additive genetic effects) was more important than specific combining ability (nonadditive genetic effects) in the yield of synthetic maize varieties. He thus suggested that S_1 lines were more valuable in evaluation of general combining ability than homozygous lines.

S_1 progeny testing has proven to be an effective method of evaluation, particularly for traits having low heritability, such as grain yield. S_1 progeny testing is used because it maintains the identity of tested genotypes, permits greater discrimination among genotypes by exposing the deleterious recessive genes, and excludes the masking effects of a tester. Several reports have shown the effectiveness of S_1 selection

in improving quantitative traits in maize populations.

Penny et al. (1967) used S_1 selection to improve five maize populations for first broad leaf feeding resistance to European corn borer [Ostrinia nubilalis (Hübner)]. Resistant genotypes were selected on the basis of S_1 resistance to artificial infestations with corn borer egg masses. Results obtained indicated that two cycles of selection were sufficient to shift the frequency of genes for resistance to a high level and that three cycles produced essentially borer-resistant varieties. Jinahyon and Russell (1969) conducted three cycles of S_1 selection in the Lancaster maize population to improve stalk-rot resistance caused by Diplodia zeae (Schw.) Lev. Progress for improvement was determined by three methods: populations themselves, testcrossed populations, and diallel crosses among populations. Significant improvement for stalk-rot resistance was observed with all three methods of evaluation. Jinahyon and Moore (1973) reported a gain in yield of 8.3% per cycle after two cycles of S_1 family selection in the 'Thai Composite' maize variety. Increased yield was accompanied by reduced stalk lodging and a slight decrease in plant and ear height. Mock and Bakri (1976) evaluated two cycles of recurrent selection for cold tolerance in 'BSSS13 (SCT)' and 'BSSS2(SCT)' maize populations. They observed gains of 8.4% and 0.6 kg per cycle for percentage of emergence and dry weight, respectively, in BSSS13(SCT). Conversely, recurrent selection based on S_1 families resulted in only 1.7%

per cycle for percentage of emergence and no gain for dry weight in BSSS2(SCT).

Other studies based on inbred family selection were conducted in comparison with other recurrent selection schemes. Koble and Rinke (1963) yield tested random S_1 lines in comparison to topcross tests with related and unrelated testers. Significant correlations between S_1 lines and topcross tests were obtained for grain yield and other agronomic traits. They suggested that selection based on S_1 line performance might replace the tedious and expensive method of topcrossing. Lonnquist and Lindsey (1964) evaluated 169 S_1 lines by three methods: selection based on S_1 lines *per se*, testcrosses with a related synthetic, and testcrosses with an unrelated tester. All evaluation procedures proved to be effective, but a slight advantage was noticed for testcrosses with an unrelated tester. In another experiment, Lonnquist (1968) reported a gain in grain yield of 4% for the S_1 lines and 15% for testcrosses involving the parental population as tester. No gain resulted from selection based on testcrosses with an unrelated tester. The observed ranges for various traits, however, were greater in lines *per se* than in testcrosses.

A critical comparison of S_1 and testcross performance for yield and other traits was made by Genter and Alexander (1962) in four synthetic varieties. Although the S_1 test resulted in lower mean yields than the testcross yields, the ranges of S_1 mean and variance were greater than those observed in

testcrosses for all traits. They concluded that selection based on S_1 progenies should be more reliable than selection based on testcrosses. The S_1 progenies also showed less genotype-environment interaction. In another study, Genter and Alexander (1966) reported the results of two cycles of S_1 progeny testing and testcross selection initiated in the 'Corn Belt Southern Synthetic' variety. They obtained 31.4% increase in yield for selfing series versus 17.9% for the testcross series. More productive crosses were obtained from the S_1 series, but this relationship decreased with each succeeding cycle of selection.

Carangal et al. (1971) compared the effectiveness of S_1 family selection and testcross progeny performance after two cycles of recurrent selection in 'Minnesota Synthetic A' maize variety. In the first cycle, the testcrosses outyielded the S_1 lines, but the range in mean yield and genetic variance for all traits was greater for S_1 than for testcross evaluation. In the second cycle, however, mean performance of selection based on progenies was not different from selection based on testcrosses. A slight yield superiority was observed for the population selected on the basis of testcrosses. They also found that S_1 progeny evaluation was more effective than testcross evaluation for yield improvement, but both methods were equally effective with regard to combining ability. The greater range in mean yield distribution and genetic variance provided a basis for the rapid improvement of populations by

S_1 progeny evaluation. Hence, improvement of population *per se* would be attained most efficiently by S_1 evaluations, whereas improvement in combining ability would be slightly higher with testcross evaluations.

Burton et al. (1971) compared half-sib and S_1 progeny testing procedures conducted for four cycles in the Krug (BSK) Synthetic variety. Evaluations were made using five populations (C0, CS2, and CS4 for selfing series and HTC2 and HTC4 for testcrossing series) that were selfed, sibbed, testcrossed to four single-cross testers, and crossed in a diallel series. Results obtained indicated that both methods of recurrent selection improved the mean yield and the general combining ability of Krug (BSK), but S_1 selection seemed to be superior to half-sib selection (i.e., 38.7% vs 12.0% for selfed, 16.3% vs 6.2% for sibbed, and 10.6% vs 5.7% as average of four single-cross testcrosses). The diallel series exhibited heterosis which indicated that the two methods developed populations that were selected for different genes.

Genter (1973) evaluated two cycles of recurrent selection based on S_1 and testcross progeny yield in two maize synthetics: 'VCBS' and 'VLE'. S_1 selection was more effective than testcross selection in increasing yield and combining ability of VCBS synthetic (14.3% vs 2.7%), but neither selection method resulted in significant yield change in the advanced populations of VLE synthetic.

Goulas and Lonnquist (1976) conducted two cycles of

recurrent selection for intrapopulation improvement in a composite maize variety using half-sib and S_1 evaluation methods simultaneously. Significant improvement resulted from combined selection and grain yield increased by 7 and 24% after the first and second cycles of selection, respectively. Ear height and prolificacy increased while grain moisture decreased. They concluded that combined half-sib and S_1 evaluation provides the basis for an increase in frequency of desirable alleles and allelic combinations at a greater rate than either method conducted individually.

Genetic Variability

The determination of genetic variability is based upon the partition of the phenotypic value of a trait into hereditary, or genotypic, effects and environmental effects. This can be symbolized as:

$$P = G + E + GE \quad ,$$

where P is the phenotypic value, G is the genotypic effect, E is environmental effect, and GE is the effect of the interaction between genotype and environment. Similarly, the phenotypic variance is the sum of the variances of genotypic, environmental, and interaction effects:

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2 + \sigma_{GE}^2$$

Genotypic variance was further partitioned by Fisher (1918) into additive genetic variance (σ_A^2), due to average

effects of the alleles at a locus, dominance variance (σ^2_D), due to intra-allelic interactions, and epistatic variance (σ^2_I), due to inter-allelic interactions or nonadditivity among loci. Cockerham (1954) extended the treatment of epistatic variance by considering several components: additive x additive (σ^2_{AA}), additive x dominance (σ^2_{AD}), dominance x dominance (σ^2_{DD}), ...

$$\sigma^2_I = \sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD} + \ldots.$$

Additive genetic variance is the portion of the total genetic variance that is fixable through selection and, thus, provides an indication of selection effectiveness. Therefore, progress from selection depends on the amount and type of genetic variances present in the population.

Hull (1945) postulated that the genetic variance in open-pollinated maize varieties was mainly nonadditive and, thus, progress from mass selection could not be expected. He stated that previous selection in Corn Belt varieties had largely dissipated the additive genetic variance and was the primary reason mass and ear-to-row selection were ineffective for increasing grain yield in maize varieties.

After the publication of papers on genetic mating designs by Comstock and Robinson (1948, 1952), research was conducted in various maize populations to investigate the nature of genetic variances. In most instances, additive variance has been found to be of greater importance than dominance variance

(Sprague and Eberhart, 1977). Other studies that used more complex mating designs that permitted the estimation of digenic and trigenic types of epistasis showed that epistatic variance was negligible (Eberhart et al., 1966; Chi et al., 1969; Wright et al., 1971; Silva and Hallauer, 1975).

The basic objective of any recurrent selection program is to gradually increase the frequency of desirable alleles and increase performance of the population. This may lead to reduced genetic variability and, thus, preclude further gain from selection. Therefore, a mechanism for maintenance of genetic variability is needed to permit several cycles of selection. Among the phases of each cycle of recurrent selection, recombination of selected genotypes is conducted to maintain genetic variability in the population undergoing selection.

Several workers have been concerned about the erosion of genetic variability after several cycles of recurrent selection. Results of two cycles of recurrent selection in two high yielding Krug synthetics, reported by McGill and Lonnquist (1955), showed a marked reduction in genetic variability. Conversely, Penny et al. (1963) presented data of genetic variance estimates from various recurrent selection programs conducted in Iowa indicating that the level of genetic variability was substantially maintained over several cycles of recurrent selection.

Lonnquist et al. (1966) observed no change in additive

genetic variance after six cycles of mass selection in the Hays Golden maize variety. Harris et al. (1972), however, detected less variability among random S_1 lines and test-crosses extracted from two populations of Hays Golden after nine cycles of mass selection than from the original population.

Moll et al. (1977) evaluated the performances of single-cross hybrids among unselected inbred lines derived from C0 and C6 cycles of reciprocal recurrent selection. Although the single-crosses from the sixth cycles yielded 12.8% more than those obtained from the original population, variability among the single-crosses was similar for the C0 and C6 cycles.

Lantin (1980) estimated genetic variability in two maize varieties, 'BS10' and 'BS11', that are undergoing reciprocal full-sib selection. After four cycles, there was no evidence of reduced genetic variability.

Dudley (1977) analyzed 76 generations of selection for percentage of oil and protein in 'Burr's White' maize variety. He concluded that adequate genetic variability was present for both traits and further response to selection was expected in future cycles. Similar conclusions were reported by several investigators who estimated the relative change in genetic variation for yield and other quantitative traits after fewer cycles of recurrent selection (Eberhart et al., 1973; Burton et al., 1971; Darrah et al., 1972; Horner et al., 1973;

Russell et al., 1973). Hence, it seems that genetic variability has been maintained in most recurrent selection programs, particularly in the earlier cycles of selection.

MATERIALS AND METHODS

Plant Materials and Field Procedures

Evaluation of mass-selection

The 'Krug' (BSK) maize variety used was a strain of the open-pollinated variety 'Krug Yellow Dent' designated as 'Krug High I Syn 3', which was developed at the Nebraska Agricultural Experiment Station by J. H. Lonnquist (1949). It was developed from eight S_1 lines selected on the basis of topcross yields; the eight S_1 lines were intercrossed in isolation for three generations. Krug High I Syn 3 was random mated at Iowa and coded 'BSK'.

Mass selection for grain yield was initiated in BSK in 1961 and continued until 1976 after 14 cycles of mass selection had been completed. The field techniques and procedures used for individual plant selection in each cycle of selection were similar to those developed by Gardner (1961). The only modification of Gardner's method was the use of a rectangular basic selection unit instead of a square unit. Also, irrigation was not provided in any of the cycles of selection.

The isolation field for each cycle was partitioned into 100 sub-blocks, or grids, each with two rows including 40 competitive plants. Within each grid, 8 to 12 ears were phenotypically selected. The selected ears were artificially dried to uniform moisture level (about 8%), shelled, and weighed.

Equal quantities of seed from the three highest yielding ears for each sub-block were composited to form two bulks; one bulk was used for planting the subsequent cycle of selection, and the second bulk was put in cold storage for future use. Hence, the selection intensity was 7.5% in all cycles of selection.

In 1976, remnant seeds of the even cycles of selection (i.e., Krug(M)C2, Krug(M)C4, ..., Krug(M)C14) were increased by sibbing and two sets of testcrosses were produced: (1) Krug(BSK)C0, the parental population or a related broad-genetic base tester; and (2) the inbred line B73, an unrelated narrow-genetic base tester. Additionally, the following entries were included in the experiments as duplicate entries to increase the precision of the regression estimates: KrugC0, Krug(M)C14, KrugC0 x Krug(M)C2, KrugC0 x Krug(M)C14, B73 x KrugC0, and B73 x Krug(M)C14. The single-cross hybrid, B73 x M017, was included as a check entry.

The 30 entries were evaluated at five Iowa locations in 1978 (Nashua, Kanawha, Ames Agronomy Research Center, Ames Atomic Energy Farm, and Martinsburg), at three locations in 1979 (Nashua, Ames Agronomy Research Center, and Ankeny), and two locations in 1980 (Ames Agronomy Research Center and Ankeny). Each experiment was arranged in a randomized complete block design with three replications in 1978 and 1979 and five replications in 1980. Plots included two rows 508 cm long spaced 76 cm at each location, except at Martinsburg in 1978 where plots measured 518 cm x 193 cm. All plots were

overplanted and thinned to 34 plants per plot.

Data were collected for the following traits:

Stand: The number of plants in each plot was recorded before or during anthesis. Plot stand counts were converted to thousands of plants per hectare.

Date of silk: Silking date was recorded as number of days from July 1 when 50% of the plants in each plot showed incipient silk-emergence on the tip of their primary ears.

Ear height: Twenty competitive plants from each plot were measured to the nearest centimeter from ground level to the node of the primary ear. Average ear height was determined for each plot and used in the analysis of variance.

Root and stalk lodging: The number of plants that were visually inclined from the vertical by more than 30^{o} were considered as root lodged plants. Plants with broken stalks below the top ear were counted as stalk lodged plants. The recorded numbers for these two traits in each plot were expressed as percentage of the stand in the plot.

Ears per plant: Ears from each plot of hand-harvested experiments were counted before shelling and the total number of ears was divided by stand of the plot to obtain the number of ears per plant.

Dropped ears: At harvest, dropped ears were gleaned and the number expressed as percentage of the total number of plants for each plot.

Grain yield: Husked ears from hand-harvested experiments

were dried to uniform moisture content (about 8%), shelled, weighed to the nearest gram, and converted to quintals per hectare. At Nashua in 1979 and Ankeny in 1979 and 1980, unhusked harvested ears from each plot were shelled by Massey Ferguson 205 combine to obtain grain yield. Moisture content was determined using a portable moisture tester attached on the combine. Grain yield per plot was adjusted for stand and moisture at 15.5% and expressed in quintals per hectare.

Evaluation of S_1 lines

Prior to mass selection, two recurrent selection programs were initiated in the Krug(BSK) variety and conducted concurrently. Recurrent selection was based on (1) S_1 progeny evaluation and (2) half-sib family evaluation using either double-cross hybrids, or inbred lines as testers. The double-cross (WF9 x M14) x (B14 x W22) served as testers during the three first cycles. Testers for cycles 4 and 5 were the two single crosses (WF9 x W22 and B14A x M14). A related inbred line, 'Krug 755', was the tester in the sixth cycle of selection, and the unrelated inbred line, B73, was used as tester in the subsequent cycles of the half-sib recurrent selection program. Eight cycles have been completed in each one of these two recurrent selection programs.

In 1979, a random sample of 500 plants was grown in the nursery at the Ames Agronomy Research Center for each

one of the following four populations: the original Krug C0, the 14th cycle of mass selection [BSK(M)C14], the 8th cycle of half-sib selection [BSK(HI)C8], and the 8th cycle of S_1 progeny evaluation [BSK(S)C8]. At flowering, approximately 250 plants were selfed in each one of these four populations to produce unselected S_1 lines. Only 100 well-filled ears from each population were individually shelled to obtain seeds for evaluation of S_1 lines.

The 400 S_1 lines (100 from each of the four populations) were evaluated in 1980 at four Iowa locations: Ames Agronomy Research Center, Ames Hinds Farm, Ankeny, and Martinsburg. The entries were grouped into 10 sets of 40 S_1 lines, each set including 10 lines from each population. Each line was replicated twice and the sets with the same entries were arranged adjacently in each experiment. The populations were randomized within each replication, and the lines were randomized within each population. Single-row plots of 508 x 76 cm were used for each experiment. All plots were over-planted and thinned to 17 plants per plot for each S_1 line.

Data were collected for eight traits for the 400 S_1 lines: stand count, silking date, ear height, root and stalk lodging, ear number, grain yield, and grain moisture. Stand was recorded in each experiment. Date of silk and ear height were measured at Ames Agronomy Research Center and Ames Hinds Farm, and roots and stalk lodging were measured in all experiments, except Ames Hinds Farm. Ear number was recorded

at Ames Agronomy Research Center and Ames Hinds Farm. All plots at the two Ames locations were hand harvested and dried to uniform moisture content (about 8%) before shelling. Moisture content was measured at Ankeny and Martinsburg where the unhusked harvested ears from each plot were shelled by the Massey Ferguson 205 combine to obtain grain weight; shelled grain weights were obtained and adjusted to 15.5% moisture content.

Statistical Analyses

Response to mass selection

Analyses of variance were performed for each trait at each location using a randomized complete block design. The following linear model was used:

$$Y_{ij} = \mu + T_i + \beta_j + e_{ij} \quad ,$$

where:

Y_{ij} = observed value of the ith entry in the jth block;

μ = overall mean effect;

T_i = effect of ith entry, i = 1,2, ..., 30;

β_j = effect of jth block, u = 1, 2, 3,;

e_{ij} = error term associated with ijth observation;

and $T_i \sim$ NIK $(0, K_T^2)$; and

$e_{ij} \sim$ NID $(0, \sigma_e^2)$

The format of this analysis of variance is shown in Table 1.

Table 1. Analysis of variance and expected mean squares of randomized complete block design in one experiment

Source of variation	d.f.	Mean squares	Expected mean squares
Replications (b)	$(b-1)^a$		
Entries (t)	(t-1)	M_2	$\sigma_e^2 + bK_T^2$
Error	(b-1)(t-1)	M_1	σ_e^2
Total	bt-1		

[a]b = 3 in the experiments of 1978 and 1979, and b = 5 in the 1980 experiments.

Data for traits recorded in several experiments were combined across locations (Table 2). Data for the Ankeny 1979 experiment were discarded before harvest because of nitrogen deficiency and severe stalk lodging that occurred during early flowering. The following linear model was used for the combined analysis of variance for each trait.

$$Y_{ijk} = \mu + L_i + \beta_{ij} + T_k + (LT)_{ik} + e_{ijk} \quad ,$$

where:

Y_{ijk} = observed value of kth entry in the jth replication of the ith location;

μ = overall mean effect;

L_i = effect of the ith location;

β_{ij} = effect of the jth replication within the ith location;

Table 2. Analysis of variance and expected mean squares of a randomized complete block design combined over locations

Source of variation	d.f.	Mean squares	Expected mean squares
Locations (L)	$(\ell-1)$	M_5	$\sigma_e^2 + \sigma_{B/L}^2 + bt\sigma_L^2$
Replications/L	$(b-1)\ell$[a]	M_4	$\sigma_e^2 + t\sigma_{B/L}^2$
Entries (T)	$(t-1)$	M_3	$\sigma_e^2 + b\sigma_{TL}^2 + b\ell K_T^2$
L x T	$(\ell-1)(t-1)$	M_2	$\sigma_e^2 + b\sigma_{TL}^2$
Pooled error	$(b-1)(t-1)\ell$	M_1	σ_e^2
Total	$\ell bt-1$		

[a]Only three reps of the 1980 experiments were used for the combined analysis.

T_k = effect of the kth entry;

$(LT)_{ik}$ = interaction effect between ith location and kth location;

e_{ijk} = experimental error;

and $L_i \sim$ NIK $(0, \sigma_L^2)$;

$T_k \sim$ NID $(0, K_T^2)$; and

$e_{ijk} \sim$ NID $(0, \sigma_e^2)$.

The entries were partitioned into four groups, each group including seven or eight entries. Group 1 included the unselected Krug population (C0) and the seven even cycles of mass-selected populations (from C2 to C14). Groups 2 and 3

included the testcrosses using Krug(BSK)C0 and the inbred line, B73, as testers, respectively. Group 4 included the duplicate entries and the check entry, B73 x Mo17. Hence, groups 1 and 3 included eight entries whereas groups 2 and 4 included seven entries.

The least squares analysis proposed by Eberhart (1964) was applied to the three first groups to obtain the estimates of genetic progress from mass selection. The following linear models were used:

$$C_{0J} = m_0 + b_{0J} + e_{0J}$$

where:

J = 0,2,...,14 for the populations per se; and

$$C_{00} x C_{0J} = m_0 + b_{1J} + e_{1J}$$

where:

J = 2,4,...,14 for the testcrosses using Krug(BSK)C0 as tester; and

$$C_{10} x\ C_{0J} = m_1 + b_{2J} + e_{2J}$$

where:

J = 0,2,...,14 for the testcrosses using the inbred line, B73, as tester.

The parameters included in the models are:

J = cycle of selection within the Krug(BSK)M;

m_0 = mean of parental Krug(BSK)C0;

m_1 = mean of Krug(BSK)C0 x B73;

b_0 = regression coefficient in the 1st group;

b_1 = regression coefficient in the 2nd group;

b_2 = regression coefficient in the 3rd group; and

e_{IthJ} = deviation from linear regression in the Ith group.

Table 3 shows the partitioning of the degrees of freedom for entries for each source of variation.

Table 3. Combined analysis of variance for 30 entries in (ℓ) locations and partition of entries sum of squares into linear regression coefficients and deviations from linear regression

Source of variation	d.f.	
Locations (ℓ-1)	8	
Replications/locations (b-1)ℓ[a]	18	
Entries (t-1)	29	
Group 1 (populations per se)		7
Linear		1
Deviations		6
Group 2 (populations x C0)		6
Linear		1
Deviations		5
Group 3 (populations x B73)		7
Linear		1
Deviations		6
Group 4		6
Among groups		3
Entries x locations (t-1)(ℓ-1)	232	
Pooled error ℓ(b-1)(t-1)	522	
Total (bℓt-1)	809	

[a]b = 3 for all the experiments.

Estimation of genetic variability

Analysis of variance of data for the S_1 progenies for each trait pooled over sets for each environment was performed according to the following model:

$$Y_{ijk} = \mu + S_i + \beta_{ij} + L_{ik} + e_{ijk} \quad ,$$

where:

Y_{ijk} = observed value for the kth line in the jth replication within the ith set;

μ = overall mean;

S_i = effect of the ith set, i = 1,2,...,10;

β_{ij} = effect of the jth replication within the ith set, j = 1,2;

L_{ik} = effect of the kth line within the ith set, k = 1,2,...,40;

e_{ijk} = experimental error;

and $L_{ij} \sim (0, \sigma_L^2)$; and $e_{ijk} \sim (0, \sigma^2)$.

In each analysis of variance, the variation due to lines was partitioned into the following components: (1) among the CO lines (P_1), (2) among lines of BSK(M)C14 or P_2, (3) among lines of BSK(HI)C8 or P_3, (4) among lines of BSK(S)C8 or P_4, and (5) among populations (P). The among population sum of squares was further partitioned into three orthogonal comparisons: (1) CO lines versus lines of (M)C14, (HI)C8, and (S)C8; (2) (M)C14 versus (HI)C8 and (S)C8 lines; and (3) (HI)C8 lines versus (S)C8 lines. The format of the analysis of variance

of S_1 lines for each environment is included in Table 4.

Data for each trait also were analyzed combined across environments. The linear model used for the combined analyses of variance was:

$$Y_{ijk\ell} = \mu + E_i + S_j + B_{ijk} + L_{j\ell} + (EL)_{ij\ell} + e_{ijk\ell} \quad ,$$

where:

$Y_{ijk\ell}$ = observed value for the ℓth line in the kth replication within the jth set in the ith environment;

μ = overall mean effect;

E_i = effect of the ith environment, i = 1,2,3,4;

S_j = effect of the jth set, j = 1,2,...,10;

B_{ijk} = effect of the kth replication within the jth set in the ith environment, k = 1,2;

$L_{j\ell}$ = effect of the interaction between the ith environment and the ℓth line within the jth set;

$e_{ijk\ell}$ = experimental error;

$E_i \sim$ NID $(0, \sigma^2_E)$; $L_{j\ell} \sim$ NID $(0, \sigma^2_L)$;

$(EL)_{ij\ell} \sim$ NID $(0, \sigma^2_{EL})$; and $e_{ijk\ell} \sim$ NID$(0, \sigma^2)$.

The line sum of squares from the combined analysis was partitioned into population components that were similar to the analysis for each environment. In addition, corresponding partitions of the environment x line interactions also were performed. Sources of variation, degrees of freedom, mean squares, and expected mean squares for the combined analysis

Table 4. Analysis of variance of S_1 lines pooled over sets for each environment

Source of variation	d.f.[a]	Mean squares	Expected mean squares
Sets	$(s-1) = 9$		
Rep/sets	$s(b-1) = 10$		
Lines/sets	$s(\ell-1) = 390$	M_2	$\sigma^2 + 2\sigma^2_L$
C0 (P_1)[b]	90	M_{21}	$\sigma^2 + 2\sigma^2_{P_1}$
M (P_2)	90	M_{22}	$\sigma^2 + 2\sigma^2_{P_2}$
HI (P_3)	90	M_{23}	$\sigma^2 + 2\sigma^2_{P_3}$
S (P_4)	90	M_{24}	$\sigma^2 + 2\sigma^2_{P_4}$
Among populations (P_n)	30	M_{25}	$\sigma^2 + 2\sigma^2_P$
P_1 vs P_2,P_3,P_4	10	M_{251}	$\sigma^2 + 2K^2_{C1}$
P_2 vs P_3,P_4	10	M_{252}	$\sigma^2 + 2K^2_{C2}$
P_3 vs P_4	10	M_{253}	$\sigma^2 + 2K^2_{C3}$
Pooled error	$s(b-1)(\ell-1) = 390$	M_1	σ^2
Total	$(sb\ell-1) = 799$		

[a] s = number of sets = 10; b = number of replications = 2; and ℓ = number of lines per set = 40.

[b] P = population, where C0, M, HI, and S are original BSK, 14th cycle of mass, 8th cycle of half-sib, and 8th cycle of S_1 selections, respectively.

of variance are shown in Table 5.

The F-test of significance in Table 4 was determined by testing the lines source of variation and its components against the pooled error mean squares. In the combined analysis (Table 5), line mean squares were tested against line x environment interaction mean squares, and the line components tested against the corresponding line x environment interaction mean squares. The interaction mean squares were tested against the pooled error mean squares.

Estimates of genotypic variance associated with each population were obtained by equating mean squares with expected mean squares and solving for $\sigma^2_{P_n}$. For example, for the P_1 population for one environment,

$$\hat{\sigma}^2_{P_1} = \frac{M_{21} - M_1}{b} .$$

Likewise, from the combined analyses, estimates of genotypic variance for a given population were obtained by subtracting the corresponding interaction mean squares of the populations and dividing by the number of replications and environments. For example, the genetic variance among lines of the mass-selected population (P_2) in the combined analysis (Table 5) was estimated as follows:

$$\hat{\sigma}^2_{P_2} = \frac{M_{32} - M_{22}}{be} .$$

Standard errors of the estimates of the variance

Table 5. Analysis of variance of S_1 lines pooled over sets and combined across environments

Source of variation		d.f.[a]	Mean squares	Expected mean squares
Environment (E)	e-1	3		
Set/environment	(s-1)e	36		
Rep/set/environment	(b-1)se	40		
Lines (L)/set	(ℓ-1)s	390	M_3	$\sigma^2 + 2\sigma^2_{LE} + 8\sigma^2_L$
CO (P_1)[b]	(ℓ/4-1)s	90	M_{31}	$\sigma^2 + 2\sigma^2_{P_1E} + 8\sigma^2_{P_1}$
M (P_2)	(ℓ/4-1)s	90	M_{32}	$\sigma^2 + 2\sigma^2_{P_2E} + 8\sigma^2_{P_2}$
HI (P_3)	(ℓ/4-1)s	90	M_{33}	$\sigma^2 + 2\sigma^2_{P_3E} + 8\sigma^2_{P_3}$
S (P_4)	(ℓ/4-1)s	90	M_{34}	$\sigma^2 + 2\sigma^2_{P_4E} + 8\sigma^2_{P_4}$
Among populations (P_n)		30	M_{35}	$\sigma^2 + 2\sigma^2_{PE} + 8\sigma^2_p$
P_1 vs P_2 + P_3 + P_4		10	M_{351}	$\sigma^2 + 2K^2_{C1E}$
P_2 vs P_3 + P_4		10	M_{352}	$\sigma^2 + 2K^2_{C2E}$
P_3 vs P_4		10	M_{353}	$\sigma^3 + 2K^2_{C3E}$

Lines x environment/set	$(\ell-1)(e-1)s$	1170	M_2	$\sigma^2 + 2\sigma^2_{LE}$
P_1 x environment	$(\ell/4-1)(e-1)s$	270	M_{21}	$\sigma^2 + 2\sigma^2_{P_1E}$
P_2 x environment	$(\ell/4-1)(e-1)s$	270	M_{22}	$\sigma^2 + 2\sigma^2_{P_2E}$
P_3 x environment	$(\ell/4-1)(e-1)s$	270	M_{23}	$\sigma^2 + 2\sigma^2_{P_3E}$
P_4 x environment	$(\ell/4-1)(e-1)s$	270	M_{24}	$\sigma^2 + 2\sigma^2_{P_4E}$
P x environment	$(4-1)(\ell/4-1)$	90	M_{25}	$\sigma^2 + 2\sigma^2_{PE}$
P_1 vs $P_2 + P_3 + P_4$ + environment		10	M_{251}	$\sigma^2 + 2K^2_{C1E}$
P_2 vs $P_3 + P_4$ x environment		10	M_{252}	$\sigma^2 + 2K^2_{C2E}$
P_3 vs P_4 x environment		10	M_{253}	$\sigma^2 + 2K^2_{C3E}$
Pooled error	$(b-1)(\ell-1)es$	1560	M_1	σ^2
Total	$(rx\ell xe)-1$	3199		

[a]Number of environments = 4; number of sets = 10; number of replications = 2; and number of lines per set = 40.

[b]P = population, where C0, M, HI, and S are original BSK, 14th cycle of mass, 8th cycle of half-sib, and 8th cycle of S_1 selections, respectively.

components were computed using the following formula (Moll et al., 1960):

$$\text{S.E.}\ (\sigma^2_G) = \left(\frac{2}{C^2} \sum_i \frac{M_i^2}{df_i+2}\right)^{\frac{1}{2}} \quad ,$$

where:

M_i = the ith mean square in the function;

df_i = the degrees of freedom associated with the ith mean square; and

C = the divisor of the function of mean squares.

A variance component estimate was considered significant when its magnitude exceeded twice its standard error (Anderson and Bancroft, 1952).

Coefficients of genetic variation (GCV) were calculated using the formula:

$$\text{GCV}\ (\%) = \frac{(\sigma^2_{P_n})^{\frac{1}{2}}}{\bar{X}} \quad 100 \quad ,$$

where:

$\sigma^2_{P_n}$ = the genetic variance of the nth population; and

$\bar{X}$ = the mean of the nth population.

Comparisons of the S_1 line component of variance estimates provided genetic information on the relative variability within the original and selected populations. The genetic components of variance for the variation among S_1 lines depend on gene frequency and presence of dominance. If gene frequencies are not one-half, it is difficult to define the dominance component of variance. For F = 0 and gene

frequencies of p = q = 0.5, the S_1 line components of variance estimated $\sigma_A^2 + \frac{1}{4}\sigma_D^2$, assuming no epistasis. In absence of dominance, the S_1 line components of variance provided an estimate of σ_A^2.

Heritability on a progeny mean basis was obtained for each trait in each population in each experiment using the formula:

$$h^2 = \frac{\hat{\sigma}^2_{P_n}}{\frac{\hat{\sigma}^2}{b} + \hat{\sigma}^2_{P_n}} \quad .$$

From the combined analysis, heritability on a progeny mean basis was computed using the formula:

$$h^2 = \frac{\hat{\sigma}^2_{P_n}}{\frac{\hat{\sigma}^2}{be} + \frac{\hat{\sigma}^2_{P_nE}}{e} + \hat{\sigma}^2_{P_n}} \quad .$$

Phenotypic and genotypic correlation coefficients between pairs of traits were obtained for each population to determine the effect of the different recurrent selection schemes on the relationship of the measured traits. The following formulae from Falconer (1960) were used:

$$r_{ph_{X.Y}} = \hat{COV}_{ph_{X.Y}} / (\hat{\sigma}^2_{ph_X} \cdot \hat{\sigma}^2_{ph_Y})^{\frac{1}{2}} \quad ,$$

where:

$r_{ph_{X.Y}}$ = phenotypic correlation between traits X and Y;

$\hat{COV}_{ph_{X \cdot Y}}$ = phenotypic covariance for traits X and Y;

$\hat{\sigma}^2_{ph_X}$ = phenotypic variance of the trait X; and

$\hat{\sigma}^2_{ph_Y}$ = phenotypic variance of the trait Y.

$$r_{g_{X \cdot Y}} = \hat{COV}_{g_{X \cdot Y}} / (\hat{\sigma}^2_{g_X} \cdot \hat{\sigma}^2_{g_Y})^{\frac{1}{2}} \quad ,$$

where:

$r_{g_{X \cdot Y}}$ = genotypic correlation between traits X and Y;

$\hat{COV}_{g_{X \cdot Y}}$ = genotypic covariance for traits X and Y

$\hat{\sigma}^2_{g_X}$ = genotypic variance of the trait X; and

$\hat{\sigma}^2_{g_Y}$ = genotypic variance of the trati Y.

The observed response of the three recurrent selection procedures evaluated were compared by the predicted response using the following genetic gain formula proposed by Eberhart (1970):

$$\Delta G = \frac{k \cdot p \cdot \sigma^2_g}{y \left(\frac{\sigma^2_e}{be} + \frac{\sigma^2_{ge}}{e} + \sigma^2_g\right)^{\frac{1}{2}}} \quad ,$$

where:

ΔG = predicted genetic gain;

k = standardized selection differential;

p = parental control;

σ_g^2 = additive genetic variance;

y = number of years required per cycle;

σ_e^2 = pooled error term;

σ_{ge}^2 = genotype x environmental variance;

σ_g^2 = total genetic variance;

b = number of replications per environment; and

e = number of environments.

EXPERIMENTAL RESULTS

Response to Mass Selection for Grain Yield

Data recorded for this aspect of my study differed among experiments. For instance, eight entries that were included in the experiments prior to 1980 were not included in the 1980 experiments because of insufficient seed supplies. Also, all entries were replicated five times in the 1980 experiments whereas only three replications were included in the previous experiments. To accommodate these variations in entries and replications, three different combined analyses of variance were performed, and they are presented in Tables 6, 7, and 8.

Table 6 includes the analyses of variance combined for the 1978 and 1979 experiments (seven locations for yield) that included 30 entries, each replicated three times. Table 7 includes the combined analyses of variance for all the experiments (nine locations for yield) conducted in 1978, 1979, and 1980, but these analyses of variance were based only on the 22 entries that were included in each experiment. Entries excluded from the analyses of variance in Table 7 were: KrugCO x Krug(M)C2, KrugCO x Krug(M)C14, B73 x KrugCO, B73 x Krug(M)C14, and their duplicate entries. Because the 1978 and 1979 experiments were replicated three times at each location, the fourth and fifth replications of the 1980

Table 6. Analyses of variance for six traits of BSK(M) populations and their testcrosses based on 30 entries and continued across several locations for 1978 and 1979

Source of variation	Grain yield d.f.	Grain yield Mean squares	Ears/plant d.f.	Ears/plant Mean squares	d.f.
Locations (loc)	6	10040.85**	4	0.127**	3
Rep/loc	14	245.17	10	0.012	8
Entries	29	5582.55**	29	0.085**	29
Group 1[a]	7	237.30	7	0.002	7
Linear	1	1191.94**	1	0.003	1
Deviations	6	78.54	6	0.003	6
Group 2[a]	6	184.62	6	0.009	6
Linear	1	800.21*	1	0.014	1
Deviations	5	59.25	5	0.009	5
Group 3[a]	7	304.51	7	0.008	7
Linear	1	409.98	1	0.010	1
Deviations	6	287.16	6	0.007	6
Group 4[a]	6	7341.93**	6	0.098**	6
Among groups	3	37647.34**	3	0.58**	3
Entries x loc	172	159.32**	116	0.011*	87
Group 1 x loc	42	114.66	28	0.013*	21
Group 2 x loc	36	126.11	24	0.010	18
Group 3 x loc	42	141.58	28	0.007	21
Group 4 x loc	36	204.91**	24	0.009	18
Groups x loc	18	285.27	12	0.015*	9
Pooled error	400	101.14	290	0.008	232
CV (%)		12.2		9.3	

[a]Group 1, populations per se; group 2, populations x CO; group 3, populations x B73; group 4, remainder.

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Root lodging	Stalk lodging		d.f.	Silk date	d.f.	Ear height	Dropped ears
Mean squares	Mean squares		d.f.	Mean squares	d.f.	Mean squares	Mean squares
161.66**	320.13**		2	719.28**	1	17230.02**	107.42*
4.12	6.56		6	3.88	4	750.12	88.58
12.76	19.32**		29	64.55**	29	677.09**	21.73
5.09	5.56		7	9.55**	7	696.74**	7.97
1.56	23.12*	ℓ	1	27.12**	1	3742.20**	-
5.64	4.90	q	1	19.14**	6	199.25	-
		d	5	4.43			
4.20	7.82		6	1.83	6	317.71**	8.45
3.65	2.76		1	2.89	1	1320.48**	-
4.30	8.88		5	1.63	5	116.32	-
8.77	3.23		7	2.66*	7	268.46*	3.33
6.81	3.51		1	12.71**	1	1240.89**	-
9.08	3.36		6	1.15	6	104.20	-
32.15*	35.69*		6	87.02**	6	1216.80**	24.65
18.35*	79.29*		3	417.78**	3	1403.92**	117.50
8.64**	4.46		58	0.93	29	64.18	17.74
8.28*	4.85		14	1.46	7	96.76	19.84
3.04	4.78		12	0.94	6	42.91	18.25
8.68*	4.78		14	0.63	7	56.85	12.80
8.54*	4.80		12	0.82	6	5.52	11.39
20.80	1.49		6	0.59	3	145.55**	36.03
4.80	4.24		170	1.07	110	48.34	18.87
24.6	21.8			3.7		4.1	115.3

Table 7. Analyses of variance for seven traits of BSK(M) populations and their testcrosses based on 22 entries and combined across experiments conducted in 1978, 1979, and 1980

Source of variation	Grain yield d.f.	Grain yield Mean squares	Ears/plant d.f.	Ears/plant Mean squares	d.f.
Locations (loc)	8	6298.72**	5	0.099**	4
Rep/loc	18	222.94	12	0.007	10
Entries	21	7704.25**	21	0.082**	21
Group 1[a]	7	258.44	7	0.002	7
Linear	1	1125.09**	1	0.005	1
Quadratic Deviations	6	114.07	6	0.0007	6
Group 2[a]	4	188.95	4	0.004	4
Linear	1	471.15	1	0.002	1
Deviations	3	94.63	3	0.005	3
Group 3[a]	5	163.03	5	0.008	5
Linear	1	619.30	1	0.03*	1
Deviations	4	50.22	4	0.003	4
Group 4[a]	2	17585.21**	2	0.122*	2
Among groups	3	41079.6**	3	0.470**	3
Entries x loc	168	174.98**	105	0.011*	84
Group 1 x loc	56	158.95	35	0.014**	28
Group 2 x loc	32	117.12	20	0.007	16
Group 3 x loc	40	195.92**	25	0.006	20
Group 4 x loc	16	157.81	10	0.020**	8
Groups x loc	24	266.07	15	0.010	12
Pooled error	378	125.60	252	0.008	210
CV (%)		13.6		9.4	

[a]Group 1, populations per se; group 2, populations x CO; group 3, populations x B73; group 4, remainder.

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Root lodging	Stalk lodging		Silk date		Ear height		Moisture
Mean squares	Mean squares	d.f.	Mean squares	d.f.	Mean squares	d.f.	Mean squares
125.53**	522.70**	3	716.61**	2	23001.68**	1	7512.25**
70.50	6.78	8	2.01	6	289.38	4	24.15
26.00**	18.52**	21	99.90**	21	940.77**	21	7.53
3.78	4.53	7	18.47**	7	912.43**	7	5.06*
2.85	14.55	1	77.31**	1	4915.09**	1	24.54*
		1	30.60**	1	1219.86**		
4.05	2.85	5	5.77	5	49.98	6	3.30
9.11	1.3	4	2.83	4	470.19**	4	2.87
9.30	0.06	1	3.84	1	1245.46**	1	2.10
				1	342.09**		
9.15	5.21	3	3.00	2	166.50**	3	3.12
5.95	1.94	5	2.90**	5	80.20	5	5.68
7.80	1.23	1	6.17*	1	237.69	1	12.66
5.45	2.04	4	2.09	4	40.95	4	3.96
153.13**	72.09**	2	270.86**	2	3088.59**	2	27.00**
48.94	66.01**	3	467.00**	3	1636.80**	3	9.58
10.42**	4.21	63	2.20**	42	66.15	21	4.78
7.80*	4.21	21	2.74	14	55.72	7	3.63
3.34	3.43	12	1.47	8	23.79	4	6.91
8.65*	3.95	15	0.96	10	58.55	5	5.73
16.15	8.06**	6	3.08	4	151.81	2	0.86
25.12**	6.91	9	3.36	6	102.53	3	5.65
4.71	3.59	168	1.46	126	45.74	168	4.00
23.5	22.1		4.5		4.2		7.6

Table 8. Analysis of variance for grain yield of BSK(M) populations and their testcrosses based on 22 entries combined for two experiments conducted in 1980

Source of variation	d.f.	Grain yield mean squares
Locations	1	6228.73**
Rep/locations	8	980.41
Entries	21	3701.88**
Group 1 (populations per se)	7	356.79
Linear	1	101.16
Deviations	6	399.36
Group 2 (populations x C0)	4	212.26
Linear	1	352.69
Deviations	3	165.66
Group 3 (populations x B73)	5	460.05
Linear	1	451.37
Deviations	4	461.92
Group 4 (remainder)	2	6685.68*
Among groups	3	19573.78**
Entries x locations	21	270.19
Group 1 x locations	7	237.95
Group 2 x locations	4	251.04
Group 3 x locations	5	331.24
Group 4 x locations	2	104.94
Groups x locations	3	379.40
Pooled error	168	236.04
CV (%)		17.87

* and **indicate significance at the 5 and 1% levels of probability, respectively.

experiments were not included in the combined analyses of variance shown in Table 7. The third combined analysis of variance (Table 8) included only the 1980 experiments that included five replications at each location. Grain yield was the only trait recorded in both 1980 experiments.

In the three combined analyses of variance, highly significant ($P \leq 0.01$) differences among locations were detected for all traits, except for dropped ears. The experiments were conducted at sites distributed from northern to southern Iowa, and differences in weather conditions and soil fertility were responsible for the observed differences among locations. For most of the traits (except for root lodging and dropped ears in Table 6, and grain moisture in Table 7), highly significant differences were present among entries. Differences among entries were expected because the check entry was included among the entries and two genetically different testers were used to produce the testcross populations. This was evident because of the highly significant differences among groups for all traits, except for dropped ears. Mean squares for entries x locations also were significant ($P \leq 0.05$ or $P \leq 0.01$), except for stalk lodging, silk date, ear height, grain moisture, and dropped ears. Hence, for these five traits, the entries performed consistently among experiments. For the other traits, however, comparisons between entry and entry x location variance components re-

vealed that the significant interactions resulted from large changes in magnitude of entries over locations rather than from differences in relative ranking across locations. Results of the combined analyses, therefore, were of primary interest, and analyses of variance for each individual experiment are included in the Appendix.

Partition of entries sum of squares into sum of squares for populations per se (group 1), populations x C0 (group 2), and populations x B73 (group 3) resulted in few significant mean squares, although highly significant differences were detected among groups for nearly all traits. Mean squares were significant among entries included in the fourth group for each trait, except for dropped ears and grain moisture. Because of the diversity among entries included in group 4, significant differences among entries were expected. For my study, however, this group was of limited interest.

Mean squares for grain yield, the primary trait used for mass selection, were not significant for either populations per se or testcross populations in any of the combined analyses of variance. Significant group mean squares were observed only for silking date (populations per se and populations x B73), ear height (for each group in Table 6, and populations per se and populations x C0 in Table 7), and grain moisture (for populations per se).

Relationships among cycles of selection and changes among cycles for each measured trait were investigated by

regression analyses. Testing for linearity among cycles indicated limited significant changes with cycles of selection. No linear responses were observed for ears per plant, root lodging, and dropped ears. Grain yield showed significant linear trend for populations per se (Tables 6 and 7), and populations x C0 (Table 7). Significant linear responses were obtained for populations per se grain moisture and stalk lodging (Tables 7 and 6, respectively). Silking date and ear height had divergent responses; linear responses were obtained among testcross populations using B73 as tester, while ear height also showed similar response among testcross populations using C0 as tester (Table 6). For the populations per se for silking date in Tables 6 and 7 and for populations per se and populations x C0 for ear height in Table 7, significant deviations persisted after fitting the linear model. Further testing for quadratic responses resulted in highly significant mean squares. In most instances, the deviation mean squares were not significant after fitting the linear (and quadratic) model(s). One exception was for ear height that showed a highly significant deviation term after fitting the cubic model.

Regression coefficient estimates (b), their standard errors, and coefficients of determination are summarized in Table 9. These regression coefficient estimates provided estimates of average response on a per cycle basis or gain

Table 9. Regression coefficient estimates (b), their standard errors, and coefficients of determination (R^2) for seven traits measured in KrugBSK(M) populations and their testcrosses

Traits		Populations per se (group 1) b	R^2
Grain yield (q/ha)		0.58** ± 0.18[a]	0.71
		0.50** ± 0.19	0.62
Ears/plant (no.)		-0.001 ± 0.002	0.16
		-0.001 ± 0.001	0.54
Silk date (days)	ℓ	0.53** ± 0.11	0.67
	q	-0.03** ± 0.007	
	ℓ	0.63** ± 0.13	
	q	-0.03** ± 0.009	0.79
Ear height (cm)	ℓ	1.93** ± 0.31	0.76
	ℓ	4.95** ± 0.70	0.96
	q	-0.22** ± 0.05	
Moisture (%)		-[b]	-
		0.16* ± 0.06	0.56
Root lodging (%)		0.03 ± 0.06	0.04
		0.03 ± 0.06	0.11
Stalk lodging (%)		0.11* ± 0.05	0.44
		0.07 ± 0.04	0.46

[a]The upper and bottom values refer to estimates computed on means from number of d.f.±1 for locations x 3 in Tables 6 and 7 analyses of variance, respectively.

[b]Estimates not obtained.

* and ** indicate significant difference at the 5 and 1% levels of probability, respectively.

Populations x C0 (group 2)		Populations x B73 (group 3)	
b	R^2	b	R^2
0.59** ± 0.23	0.73	0.34 ± 0.20	0.19
0.66 ± 0.33	0.62	-0.57 ± 0.32	0.76
0.003 ± 0.002	0.23	-0.002 ± 0.002	0.18
0.001 ± 0.004	0.01	0.002 ± 0.002	0.69
-0.05 ± 0.03	0.26	0.09** ± 0.02	0.65
-0.09 ± 0.06	0.66	0.09** ± 0.03	0.42
1.40** ± 0.25	0.69	1.11** ± 0.24	0.66
8.09** ± 1.76 -0.39** ± 0.11	0.47	0.61* ± 0.30	0.59
-	-	-	-
-0.09 ± 0.16	0.18	0.17 ± 0.12	0.44
0.05 ± 0.05	0.15	0.06 ± 0.07	0.11
0.12 ± 0.07	0.25	-0.09 ± 0.09	0.26
0.04 ± 0.06	0.06	0.04 ± 0.05	0.16
-0.01 ± 0.08	0.01	0.03 ± 0.06	0.13

per year for mass selection. Each cycle of mass selection can be completed in each year (assuming no recombination or using winter nursery for recombination between cycles). Due to disparities among the combined analyses of variance and data collected from each experiment, two regression values were estimated for each trait, except for grain moisture. Generally, the two estimates of regression were within the same range, as determined by their respective standard errors.

The observed and predicted responses for traits that showed significant linear (and quadratic) trend(s) are summarized in Table 10. These responses also are illustrated graphically in Figures 1 to 5. Mass selection for grain yield was moderately effective because a positive response of about one-half quintal per hectare per cycle was realized (Figure 1). Figures 2 to 5 show the correlated responses to mass selection for grain yield. Increase in grain yield was accompanied by delayed silking date (at least during the earlier cycles, Figure 2), higher grain moisture content at harvest (Figure 4), and increased ear height and stalk lodging (Figures 3 and 5, respectively). The correlated responses of mass selection for grain yield were, unfortunately, not in the desired directions for commercially grown corn.

Means, standard errors of the means, and ranges observed for the seven measured traits in each group are recorded in Table 11. Comparisons among the following three groups were

Table 10. Observed ($\bar{Y}$) and predicted ($\hat{Y}$) means for five traits of BSK(M) populations and their testcrosses

Entries	Grain yield		Ears/plant		Silk date	
	$\bar{Y}$	$\hat{Y}$	$\bar{Y}$	$\hat{Y}$	$\bar{Y}$	$\hat{Y}$
Populations per se						
KrugC0	67.61[a]	66.71	0.89	0.897	28.3	28.74[b]
	69.70	68.38	0.90	-[d]	26.7	27.00[b]
Krug(M)C2	66.09	67.87	0.89	0.895	30.3	29.68
	70.23	69.38	0.89	-	28.3	28.14
Krug(M)C4	69.37	69.03	0.90	0.893	30.6	30.40
	69.28	70.38	0.88	-	29.6	29.02
Krug(M)C6	73.02	70.20	0.90	0.891	31.0	30.89
	69.48	72.37	0.88	-	28.9	30.05
Krug(M)C8	68.21	71.36	0.88	0.889	30.0	31.16
	71.03	71.37	0.89	-	28.9	29.66
Krug(M)C10	72.67	72.52	0.91	0.887	31.9	31.20
	72.22	73.36	0.88	-	30.9	30.19
Krug(M)C12	74.04	73.68	0.88	0.885	31.0	31.02
	77.81	74.36	0.89	-	29.8	30.09
Krug(M)C14	75.16	74.85	0.87	0.883	30.6	30.61
	75.20	75.36	0.87	-	29.9	29.75
Populations x C0						
Krug(M)C2xC0	67.34	66.78	0.85	-	29.0	29.2
	--	-	--	-	--	28.7
Krug(M)C4xC0	67.43	67.95	0.87	-	29.3	29.1
	67.75	-	0.86	-	28.7	28.4
Krug(M)C6xC0	68.23	69.13	0.88	-	29.1	29.0
	67.86	-	0.88	-	28.2	28.2
Krug(M)C8xC0	71.47	70.30	0.92	-	28.4	28.9
	72.01	-	0.90	-	27.3	28.0
Krug(M)C10xC0	72.47	71.48	0.86	-	29.2	28.8
	73.71	-	0.87	-	27.8	27.8
Krug(M)C12xC0	69.79	72.65	0.87	-	29.1	28.7
	71.43	-	0.87	-	28.0	27.6
Krug(M)C14xC0	75.33	73.82	0.91	-	28.1	28.6
	--	-	--	-	--	27.4

[a]The upper and bottom values were obtained as means of d.f.+1 in Tables 6 and 7, respectively.

[b]Linear and quadratic model fitted.

[c]-- indicates the value was not observed or predicted.

[d]No significant regression coefficients estimates.

Ear height		Moisture		Root lodging		Stalk lodging	
$\overline{Y}$	$\hat{Y}$	$\overline{Y}$	$\hat{Y}$	$\overline{Y}$	$\hat{Y}$	$\overline{Y}$	$\hat{Y}$
155.3	162.6	--[c]	--	9.46	-	9.74	9.63
147.2	147.1[b]	26.06	25.67	9.92	-	8.74	-
167.0	166.5	--	--	8.37	-	10.11	9.84
156.9	156.9	25.05	25.98	9.31	-	8.94	-
170.8	170.3	--	--	9.59	-	10.35	10.06
161.6	163.3	25.76	26.29	9.81	-	9.30	-
179.0	174.2	--	--	8.53	-	9.05	10.27
176.2	172.3	27.67	26.91	10.56	-	9.04	-
185.8	178.0	--	--	10.21	-	10.24	10.49
167.3	168.7	27.08	26.60	8.94	-	8.38	-
183.8	181.9	--	--	10.00	-	11.39	10.70
173.8	174.1	28.03	27.23	10.20	-	9.07	-
185.2	185.7	--	--	9.35	-	11.32	10.41
171.7	174.1	27.25	27.54	9.67	-	10.13	-
182.0	189.6	--	--	9.01	-	10.83	11.13
173.4	172.3	27.18	27.85	10.08	-	9.72	-
162.0	159.5	-	-	9.51	-	8.73	-
--	122.3[b]	--	--	--	-	-	-
156.5	162.3	-	-	8.10	-	10.93	-
148.4	148.4	26.70	-	8.69	-	9.65	-
166.5	165.1	--	--	9.13	-	10.35	-
158.3	156.8	26.20	-	10.22	-	8.96	-
166.5	167.9	--	--	8.84	-	10.85	-
158.0	162.1	25.20	-	9.38	-	9.33	-
177.5	170.7	--	--	9.93	-	10.35	-
168.0	164.3	26.72	-	10.73	-	9.04	-
171.8	173.5	--	--	9.10	-	10.85	-
162.0	163.3	25.50	-	9.68	-	9.51	-
174.3	176.3	--	--	9.55	-	9.62	-
--	-	--	--	-	-	-	-

Table 10. (Continued)

Entries	Grain yield		Ears/plant		Silk date	
	$\bar{Y}$	$\hat{Y}$	$\bar{Y}$	$\hat{Y}$	$\bar{Y}$	$\hat{Y}$
Populations x B73						
KrugC0xB73	98.73	-	1.04	-	24.2	24.20
	--	-	--	-	--	23.03
Krug(M)C2xB73	102.90	-	1.06	-	24.8	24.30
	105.59	-	1.04	-	23.6	23.20
Krug(M)C4xB73	103.96	-	1.06	-	24.2	24.50
	107.71	-	1.05	-	23.0	23.38
Krug(M)C6xB73	102.37	-	1.02	-	24.4	24.70
	106.05	-	1.01	-	23.1	23.55
Krug(M)C8xB73	99.93	-	1.01	-	25.0	24.90
	104.27	-	1.01	-	24.0	23.72
Krug(M)C10xB73	103.09	-	1.03	-	25.0	25.10
	101.93	-	1.02	-	24.2	23.89
Krug(M)C12xB73	98.83	-	1.00	-	24.9	25.30
	101.40	-	0.99	-	23.9	24.06
Krug(M)C14xB73	110.54	-	1.05	-	25.9	25.44
	--	-	--	-	--	24.23

Ear height		Moisture		Root lodging		Stalk lodging	
$\overline{Y}$	$\hat{Y}$	$\overline{Y}$	$\hat{Y}$	$\overline{Y}$	$\hat{Y}$	$\overline{Y}$	$\hat{Y}$
158.2	157.9	-	-	7.33	-	8.74	-
--	-	--	-	--	-	--	-
164.2	160.1	-	-	9.01	-	7.90	-
154.1	-	25.43	-	8.70	-	7.46	-
162.0	162.3	-	-	7.46	-	7.44	-
155.4	-	24.83	-	7.86	-	6.95	-
159.2	164.5	-	-	8.53	-	8.53	-
153.2	-	24.93	-	9.03	-	7.64	-
167.0	166.7	-	-	9.21	-	8.87	-
158.4	-	26.68	-	8.83	-	7.93	-
168.8	169.0	-	-	8.16	-	8.91	-
161.0	-	25.35	-	7.98	-	7.82	-
166.3	171.2	-	-	7.44	-	8.38	-
158.3	-	27.20	-	7.46	-	7.36	-
179.3	173.4	-	-	9.45	-	8.72	-
--	-	--	-	--	-	--	-

Figure 1. Direct response of grain yield to mass selection in Krug(BSK) population; --- indicates X's for nine environments and —— indicates X's for seven environments

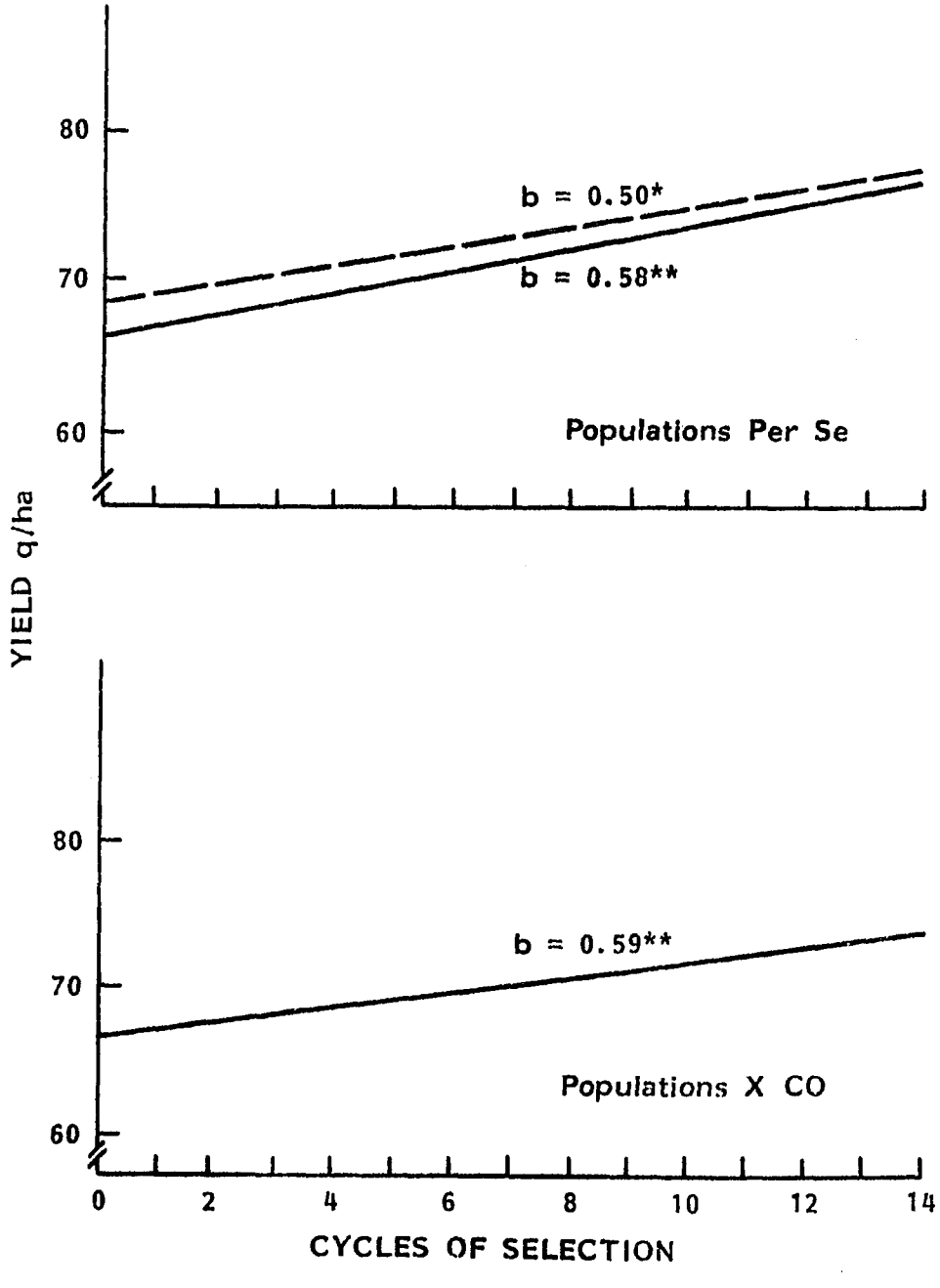
80
70
60
b = 0.50*
b = 0.58**
Populations Per Se
YIELD q/ha
80
70
60
b = 0.59**
Populations X CO
0
2
4
6
8
10
12
14
CYCLES OF SELECTION

Figure 2. Predicted correlated response of silking date to mass selection for grain yield in Krug(BSK) population; --- indicates $\bar{X}$'s for four environments and —— indicates $\bar{X}$'s for three environments

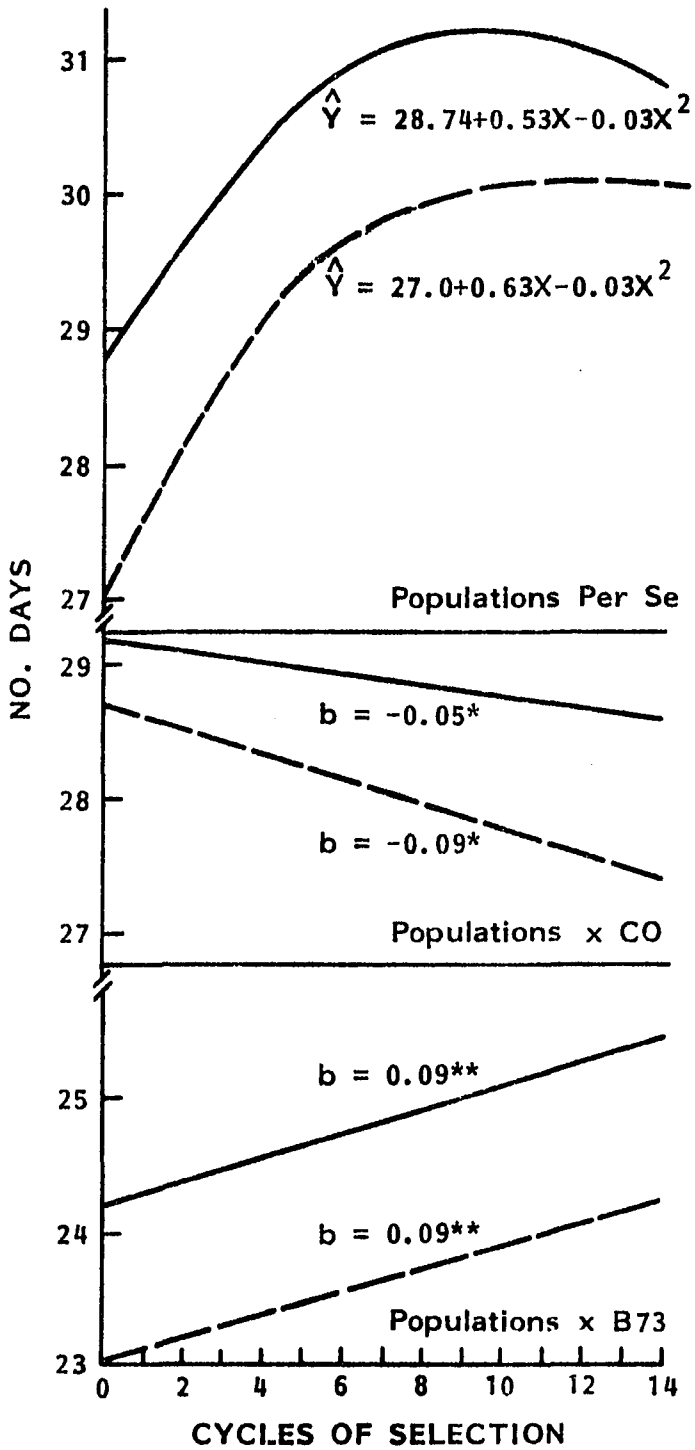
31
30
29
28
27
$\hat{Y}$ = 28.74+0.53X-0.03X^2
$\hat{Y}$ = 27.0+0.63X-0.03X^2
Populations Per Se
29
28
27
b = -0.05*
b = -0.09*
Populations x CO
25
24
23
b = 0.09**
b = 0.09**
Populations x B73
NO. DAYS
0 2 4 6 8 10 12 14
CYCLES OF SELECTION

Figure 3. Predicted correlated response of ear height to mass selection for grain yield in Krug(BSK) population; --- indicates $\bar{X}$'s for three environments and —— indicates $\bar{X}$'s for two environments

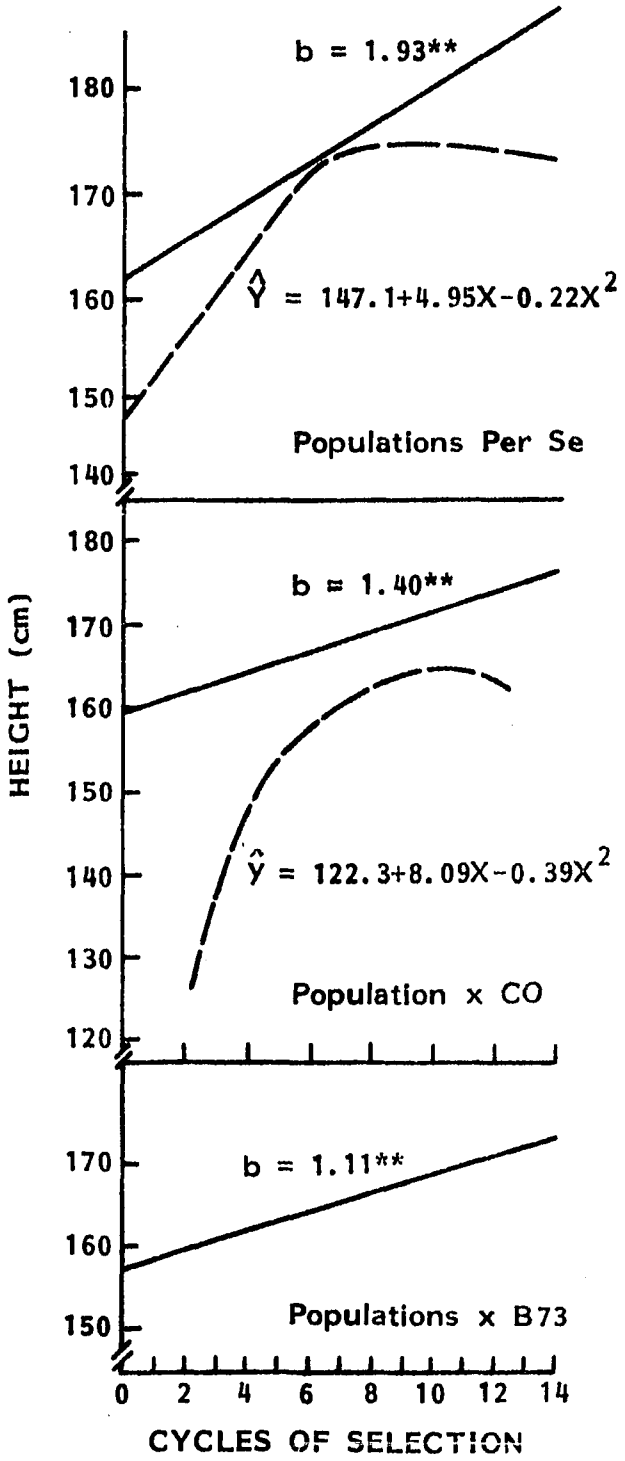
b = 1.93**
180
170
160
150
140
$\hat{Y}$ = 147.1+4.95X-0.22X^2
Populations Per Se
b = 1.40**
180
170
160
150
140
130
120
$\hat{y}$ = 122.3+8.09X-0.39X^2
Population x CO
b = 1.11**
170
160
150
Populations x B73
HEIGHT (cm)
0 2 4 6 8 10 12 14
CYCLES OF SELECTION

Figure 4. Predicted correlated response of grain moisture to mass selection for grain yield in Krug(BSK) population

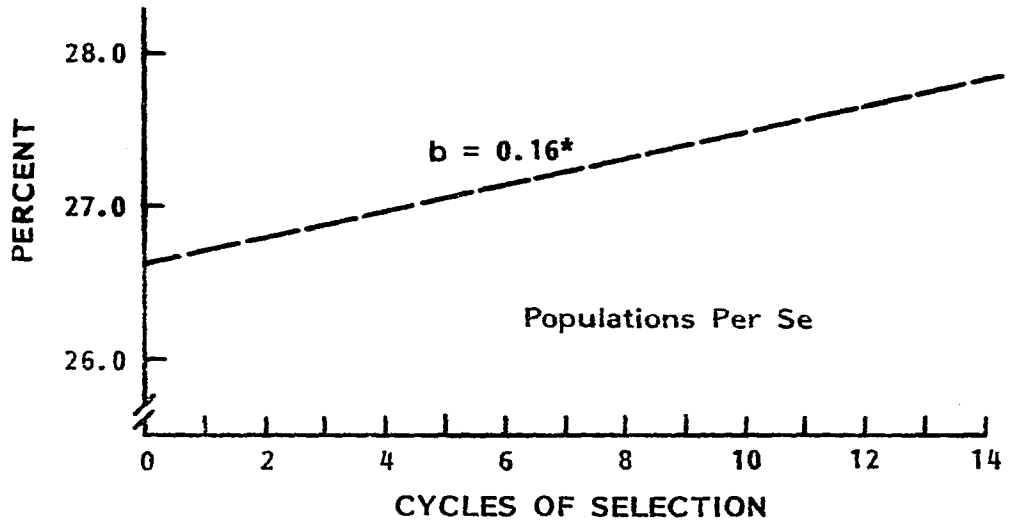
28.0
27.0
26.0
PERCENT
b = 0.16*
Populations Per Se
0
2
4
6
8
10
12
14
CYCLES OF SELECTION

Figure 5. Predicted correlated response of stalk lodging to mass selection for grain yield in Krug(BSK) population

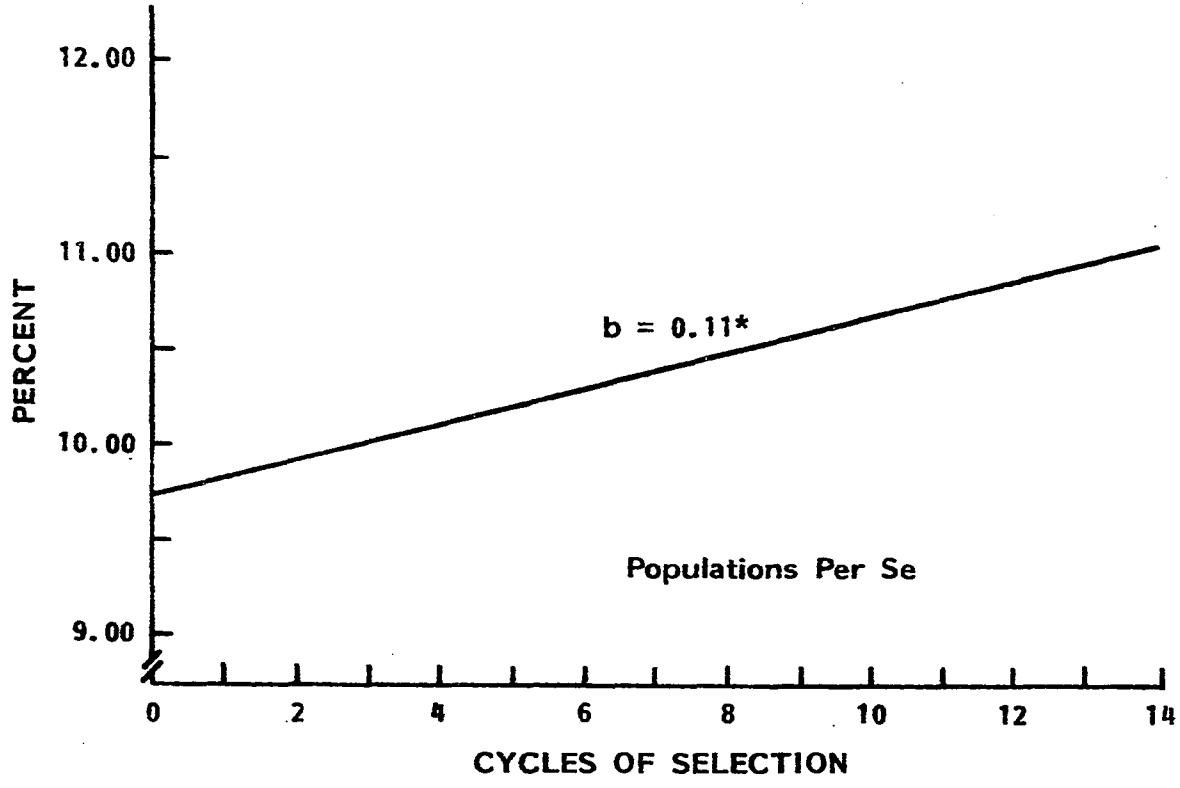
12.00
11.00
10.00
9.00
PERCENT
b = 0.11*
Populations Per Se
0
2
4
6
8
10
12
14
CYCLES OF SELECTION

Table 11. Means ($\bar{X}$), standard errors of means ($S_{\bar{X}}$), and range (R) of seven traits measured in each group of mass selected populations of Krug BSK compared in experiments conducted in 1978, 1979, and 1980

Groups		Traits		
		Grain yield	Silk date	Ear height
Group 1 (populations per se)	$\bar{X}^a$	70.78	30.46	176.11
	$S_{\bar{X}}$	±3.36	±1.04	±10.84
	R	66.1-75.2	28.3-31.9	155.3-185.8
	$\bar{X}^b$	71.87	29.24	166.01
	$S_{\bar{X}}$	±3.09	±1.28	±10.07
	R	69.3-77.8	26.7-30.9	147.2-176.2
Group 2 (populations x C0)	$\bar{X}^a$	70.30	28.89	167.89
	$S_{\bar{X}}$	±2.96	±0.45	±7.27
	R	67.3-75.3	28.1-29.3	156.5-177.5
	$\bar{X}^b$	70.55	28.00	159.00
	$S_{\bar{X}}$	±2.64	±0.51	±7.23
	R	67.8-71.0	27.3-28.7	148.4-168.3
Group 3 (populations x B73)	$\bar{X}^a$	102.54	24.80	165.63
	$S_{\bar{X}}$	±3.81	±0.56	±6.67
	R	98.7-110.5	24.2-25.9	158.2-179.3
	$\bar{X}^b$	104.49	23.63	156.73
	$S_{\bar{X}}$	±2.46	±0.49	±2.99
	R	101.4-107.7	23.0-24.2	153.2-161.0
Check (M017xB73)	$\bar{X}$	115.22	21.50	135.78

[a]Values calculated over number of d.f. ± 1 for locations source of variation x 3 in Table 6 analyses of variance.

[b]Values calculated over number of d.f. ± 1 for locations source of variation x 3 in Table 7 analyses of variance.

Traits			
Moisture	Stalk lodging	Root lodging	Ears/plant
34.75	10.38	9.32	0.89
±1.66	±0.79	±0.65	±0.01
32.1-36.9	9.05-11.39	8.37-10.21	0.87-0.91
26.76	9.17	9.81	0.89
±1.03	±0.55	±0.51	±0.01
25.1-28.0	8.38-10.13	8.94-10.56	0.87-0.90
33.36	10.24	9.17	0.88
±1.66	±0.81	±0.59	±0.03
31.4-35.9	8.73-10.93	8.10-9.93	0.85-0.92
26.06	9.30	9.74	0.87
±0.69	±0.30	±0.78	±0.02
25.2-26.7	8.96-9.65	8.69-10.73	0.86-0.90
32.68	8.44	8.32	1.03
±1.65	±0.52	±0.85	±0.02
31.1-35.1	7.44-8.91	7.33-9.45	1.00-1.06
25.74	7.53	8.31	1.02
±0.97	±0.35	±0.63	±0.02
24.8-27.2	6.95-7.93	7.46-9.03	0.99-1.05
24.01	5.38	5.07	1.005

of primary interest: populations per se, populations x CO, and populations x B73. The last two groups used a related broad genetic base tester (KrugCO) and an unrelated narrow genetic base tester (B73). For grain yield, evaluations of populations per se and testcrosses using the parental population indicated mass selection was more effective than testcrosses using B73. Mean yield for group 3, however, exceeded those for groups 1 and 2 (Table 11). Silking date and ear height were the only traits that showed significant regression values in the third group. Significant regression coefficients were obtained primarily by evaluating the populations per se. These results indicated that the KrugBSK(M) populations have many deleterious recessive genes at several loci that govern most of the evaluated traits. This hypothesis is further supported by the negative correlated responses (i.e., delayed silk emergence and maturity, increased ear height, and high incidence of stalk lodging) as mass selection progressed. Conversely, the third group (populations x B73), in addition to being higher yielding, showed marked tendencies for prolificacy, and lower ear placement. This was because of the buffering effects of dominant genes contributed by the unrelated tester, B73.

Effects of Three Recurrent Selection Methods on Genetic Variability in Krug(BSK) Population

Analyses of variance pooled over the 10 sets for the measured traits in each experiment (environment) are given in Tables 12 to 15. Table 16 shows a summary for seven traits, including the means ($\bar{X}$), standard errors of the means ($S_{\bar{X}}$), and the coefficients of variation (CV) observed in each experiment. All the coefficients of variation were within acceptable experimental limits for most traits. Relatively large CV was observed for grain yield at Ames Hinds Farm. This was ascribed to low mean performance of S_1 lines and large experimental error associated with grain yield in that experiment. In each environment, highly significant differences ($P \leq 0.01$) were detected among the 400 S_1 lines for each trait, except for stalk lodging at Ankeny, and within the 100 S_1 lines included for each one of the four populations for grain yield, silking date, ear height, and grain moisture. Similar results were obtained for ears per plant, except that the mean square of half-sib derived lines (P_3) was not significantly different from zero at Ames Agronomy Research Center (Table 12). Also, for ears per plant, only significant ($P \leq 0.05$) mean squares were obtained for the half-sib (P_3) and S_1 (P_4) derived lines at Ames Hinds Farm (Table 13). Significant differences ($P \leq 0.01$ or $P \leq 0.05$) were observed for root lodging and stalk lodging in each experiment, except

Table 12. Analyses of variance for six traits measured on 400 S_1 lines grown at Ames Agronomy Research Center in 1980 and pooled over sets

Source of variation	d.f.	Mean squares					
		Silk date	Root lodging	Stalk lodging	Ear height	Ears/ plant	Grain yield
Set	9	25.69**	335.61**	107.79**	974.46**	0.128**	1133.63**
Rep/set	10	34.86	38.01	23.24	104.78	0.031	101.75
Lines/set	390	76.70**	33.20**	22.41**	806.44**	0.095**	452.75**
CO (P_1)	90	41.86**	27.68**	17.97**	280.88**	0.086**	275.72**
M (P_2)	90	28.39**	23.81**	30.01**	426.26**	0.063**	210.55**
HI (P_3)	90	14.73**	31.08**	11.63	214.01**	0.029	174.81**
S (P_4)	90	13.07**	21.85	18.70**	232.24**	0.047**	160.92**
Among populations (P_n)	30	702.97**	118.34**	56.38**	7022.09**	0.556**	3419.78**
P_1 vs $P_2 + P_3 + P_4$	10	102.97**	118.45**	26.95*	510.83**	0.462**	2808.37**
P_2 vs $P_3 + P_4$	10	1971.22**	174.87**	112.24**	20147.14**	1.179**	7080.21**
P_3 vs P_4	10	35.31**	61.69**	29.95**	408.30**	0.026	370.75
Pooled error	390	4.71	16.51	12.14	36.37	0.029	68.93
CV (%)		8.40	32.31	29.51	5.75	19.99	21.13
Total	799						

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Table 13. Analyses of variance for four traits measured on 400 S_1 lines grown at Ames Hinds Farm in 1980 and pooled over sets

Source of variation	d.f.	Mean squares			
		Silk date	Ear height	Ears/ plant	Grain yield
Set	9	57.01**	763.49**	0.192**	1369.26**
Rep/set	10	24.24	305.88	0.105	740.60
Lines/set	390	83.89**	874.63**	0.123**	348.63**
CO (P_1)	90	50.16**	329.79**	0.076**	175.44**
M (P_2)	90	27.62**	521.62**	0.081**	143.63**
HI (P_3)	90	20.15**	201.95**	0.040*	187.32**
S (P_4)	90	15.51**	211.01**	0.036*	141.59**
Among populations (P_n)	30	750.24**	757.71**	0.903**	2588.29**
P_1 vs P_2 + P_3 + P_4	10	79.95**	54.16	0.490**	1329.67**
P_2 vs P_3 + P_4	10	2145.36**	2171.96**	2.152**	6129.75**
P_3 vs P_4	10	25.40**	47.09	0.068**	305.44**
Pooled error	390	9.60	68.30	0.028	75.44
CV (%)		12.39	7.28	24.15	32.28

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Table 14. Analyses of variance for four traits measured on 400 S_1 lines grown at Ankeny in 1980 and pooled over sets

Source of variation	d.f.	Mean squares			
		Root lodging	Stalk lodging	Grain yield	Grain moisture
Set	9	73.16**	14.89	747.59**	15.92**
Rep/set	10	7.81	21.41	563.92	11.43
Line/set	390	36.78**	12.32	478.15**	7.26**
CO (P_1)	90	28.44**	7.13	290.02**	3.43**
M (P_2)	90	32.05**	27.41**	328.78**	8.85**
HI (P_3)	90	38.44**	5.12	182.40**	5.80**
S (P_4)	90	5.90	5.86	196.89**	4.87**
Among populations (P_n)	30	163.62**	23.63**	3220.04**	25.56**
P_1 vs P_2 + P_3 + P_4	10	98.07**	7.53	4601.82**	55.78**
P_2 vs P_3 + P_4	10	214.96**	56.74**	4811.38**	9.16**
P_3 vs P_4	10	177.82**	6.61	246.93*	11.73**
Pooled error	390	15.82	9.73	116.75	2.14
CV (%)		36.49	38.83	23.19	7.54

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Table 15. Analyses of variance for four traits measured on 400 S_1 lines grown at Martinsburg in 1980 and pooled over sets

Source of variation	d.f.	Mean squares			
		Root lodging	Stalk lodging	Grain yield	Grain moisture
Set	9	34.13**	15.22**	490.05**	26.90**
Rep/set	10	9.48	9.13	161.49	10.24
Line/set	390	34.17**	21.56**	396.99**	3.34**
CO (P_1)	90	31.43**	18.51**	158.48**	2.20**
M (P_2)	90	23.75**	21.05**	225.52**	3.98**
HI (P_3)	90	28.52**	12.20**	154.39**	3.20**
S (P_4)	90	8.91*	18.68**	127.08**	1.66**
Among populations (P_n)	30	166.37**	68.88**	926.67**	10.28**
P_1 vs $P_2 + P_3 + P_4$	10	190.86**	17.19**	1831.99**	9.93**
P_2 vs $P_3 + P_4$	10	238.16**	91.36**	7459.10**	7.03**
P_3 vs P_4	10	70.10**	98.08**	202.11**	13.88**
Pooled error	390	6.76	6.52	52.41	1.07
CV (%)		24.53	21.61	17.94	5.85

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Table 16. Means ($\bar{X}$), standard deviation of means ($S_{\bar{X}}$), and coefficients of variation (CV) of seven traits measured on 100 S_1 lines of each population in each environment

Environment Populations	Traits					
	Grain yield			Moisture		
	$\bar{X}$	$S_{\bar{X}}$	CV (%)	$\bar{X}$	$S_{\bar{X}}$	CV (%)
Ames Agronomy Research Center						
CO (P_1)	29.62	3.78	25.53	-[a]	-	-
M (P_2)	27.38	4.40	32.11	-	-	-
HI (P_3)	47.89	3.11	12.96	-	-	-
S (P_4)	52.13	5.11	19.60	-	-	-
Ames Hinds Farm						
CO (P_1)	20.48	3.80	37.11	-	-	-
M (P_2)	15.29	3.91	51.05	-	-	-
HI (P_3)	34.28	3.84	22.40	-	-	-
S (P_4)	37.49	3.94	20.99	-	-	-
Ankeny						
CO (P_1)	31.25	5.22	30.89	16.46	0.93	7.98
M (P_2)	35.43	5.53	28.77	18.44	1.45	8.93
HI (P_3)	51.86	4.60	16.42	18.74	0.99	7.50
S (P_4)	53.74	5.39	18.57	17.80	0.73	5.80
Martinsburg						
CO (P_1)	30.04	4.18	25.76	17.24	0.72	5.87
M (P_2)	25.38	3.52	25.68	17.93	0.73	5.75
HI (P_3)	47.56	3.39	13.18	18.29	0.68	5.30
S (P_4)	46.36	3.30	13.17	17.29	0.63	5.17

[a]Data not recorded.

Traits								
Ears/plant			Silk date			Ear height		
$\bar{X}$	$S_{\bar{X}}$	CV (%)	$\bar{X}$	$S_{\bar{X}}$	CV (%)	$\bar{X}$	$S_{\bar{X}}$	CV (%)
0.75	0.12	23.07	27.23	1.58	8.22	107.6	4.61	6.06
0.71	0.14	27.57	22.38	1.85	7.84	129.5	4.07	4.45
0.99	0.07	9.34	22.15	1.28	8.18	90.7	3.53	5.50
0.99	0.15	21.06	20.56	1.15	7.94	91.7	3.13	4.83
0.57	0.12	29.44	26.46	2.98	15.90	116.9	4.95	6.01
0.48	0.12	34.21	33.00	2.14	9.17	138.5	7.28	7.43
0.84	0.11	17.74	21.07	1.41	10.74	94.0	4.13	5.90
0.89	0.11	17.65	19.79	1.57	11.22	99.5	5.25	7.47
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-

Table 16. (Continued)

Environment Populations	Traits					
	Root lodging			Stalk lodging		
	$\bar{X}$	$S_{\bar{X}}$	CV (%)	$\bar{X}$	$S_{\bar{X}}$	CV (%)
Ames Agronomy Research Center						
CO (P_1)	14.15	2.58	25.79	11.82	2.24	26.75
M (P_2)	13.99	3.54	35.76	13.45	2.79	29.36
HI (P_3)	12.15	2.25	26.19	10.88	1.91	24.80
S (P_4)	10.01	2.80	21.85	11.07	2.18	27.85
Ames Hinds Farm						
CO (P_1)	-	-	-	-	-	-
M (P_2)	-	-	-	-	-	-
HI (P_3)	-	-	-	-	-	-
C (P_4)	-	-	-	-	-	-
Ankeny						
CO (P_1)	12.56	3.21	36.10	7.89	1.73	30.98
M (P_2)	12.42	3.31	37.67	9.12	3.34	51.73
HI (P_3)	11.22	2.67	33.62	7.66	1.72	31.82
S (P_4)	7.41	1.68	31.98	7.45	1.55	29.45
Martinsburg						
CO (P_1)	12.99	2.17	23.62	11.84	1.76	21.05
M (P_2)	12.24	2.09	24.17	13.18	1.92	20.57
HI (P_3)	9.67	1.61	23.49	9.88	1.62	23.28
S (P_4)	7.53	1.28	23.99	12.36	1.85	21.18

at Ankeny where these two traits had nonsignificant mean squares for the S_1 (P_4) derived lines; the CO (P_1) and half-sib (P_3) derived lines showed nonsignificant differences for stalk lodging only. The S_1 derived lines showed nonsignificant mean square for root lodging at Ames Agronomy Research Center.

Comparisons between the original (P_1) and the selected populations (i.e., P_1 vs $P_2 + P_3 + P_4$) resulted in significant mean squares at either the 1 or 5% levels of probability for all traits, except for ear height (Ames Hinds Farm) and stalk lodging (Ankeny). Contrasts between S_1 lines derived from the mass selected and half-sib and S_1 selected populations (i.e., P_2 vs $P_3 + P_4$) were highly significant for all traits, except for ears per plant measured at Ames Agronomy Research Center. For most traits, contrasts between S_1 lines derived from the half-sib and S_1 selected populations (i.e., P_3 vs P_4) resulted in significant ($P \leq 0.01$ or $P \leq 0.05$) mean squares. Exceptions for these comparisons, however, were for ears per plant, ear height, and stalk lodging measured at Ames Agronomy Research Center, Ames Hinds Farm, and Ankeny, respectively.

Combined analyses of variance pooled over sets for seven traits are given in Table 17. Mean squares for environment were highly significant for grain yield, stalk lodging, ear height, and ears per plant. No significant

Table 17. Analyses of variance for seven traits measured on 400 S_1 lines combined across environments and pooled over sets

Source of variation	d.f.[a]	Mean squares: Grain yield	d.f.[b]	Mean: Root lodging
Environment (E)	3	1354.20**	2	22.55
Rep/E	36	23.30	27	3.69
Re/set/E	40	390.71	30	18.43
Lines (L)/set	390	1361.17**	390	73.42**
CO (P_1)	90	599.92**	90	55.48**
M (P_2)	90	620.11**	90	45.95**
HI (P_3)	90	462.65**	90	69.78**
S (P_4)	90	324.58**	90	17.92**
Among populations (P_n)	30	11673.42**	30	387.07**
P_1 vs $P_2 + P_3 + P_4$	10	9712.20**	10	365.16**
P_2 vs $P_3 + P_4$	10	24759.07**	10	519.89**
P_3 vs P_4	10	549.00*	10	276.15**
L X E	1170	84.44**	780	14.28**
P_1 x E	270	99.92**	180	16.04**
P_2 x E	270	96.14**	180	16.83**
P_3 x E	270	39.38	180	14.13**
P_4 x E	270	100.63**	180	4.69
P_n x E	90	240.46**	60	30.63**
P_1 vs $P_2 + P_3 + P_4$ x E	30	283.39**	20	21.11*
P_2 vs $P_3 + P_4$ x E	30	245.87**	20	54.05**
P_3 vs P_4 x E	30	192.07**	20	16.73
Pooled error	1560	78.34	1170	13.03

[a]Grain yield was recorded in four environments.

[b]Root lodging and stalk lodging were recorded in three environments.

[c]Ear height, ears per plant, moisture, and silk date were recorded in two environments.

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

squares		Mean squares			
Stalk lodging	d.f.[c]	Ear height	Ears/plant	Moisture	Silk date
95.12**	1	746.96**	0.278**	0.29	5.66
1.15	18	21.73	0.004	0.53	1.03
17.92	20	205.33	0.068	10.05	29.55
41.80**	390	1627.17**	0.19**	7.74**	155.87**
24.90**	90	561.86**	0.13**	4.20**	79.22**
44.93**	90	886.65**	0.11**	8.82**	47.04**
14.21**	90	374.21**	0.05**	6.64**	30.35**
21.68**	90	407.33**	0.06**	4.00**	24.15**
226.27**	30	14463.00**	1.38**	29.63**	1483.95**
12.90	10	929.64**	0.90**	53.47*	171.16**
604.60**	10	41722.04**	3.20**	12.52*	4226.84**
61.31	10	737.33**	0.03	22.91*	53.86**
12.15**	390	89.98**	0.03	2.20**	7.80
9.35	90	48.81	0.03	1.43	12.79**
16.73**	90	62.47	0.03	1.97	8.96
7.37	90	196.95**	0.02	2.36**	4.54
10.78	90	35.92	0.03	1.41	4.43
25.27**	30	137.24**	0.08**	7.10**	9.27*
19.38**	10	122.57*	0.05	13.34**	11.18
19.77**	10	148.07**	0.13**	2.92*	9.75
36.67**	10	141.07**	0.07*	5.05**	6.87
9.46	780	52.29	0.03	1.44	7.18

difference was detected for sets within environments for any trait. For all traits, highly significant ($P \leq 0.01$) differences occurred among the 400 S_1 lines and within the 100 S_1 lines included in each one of the four populations. Differences among lines were expected because the 400 tested S_1 lines were derived from populations that had been under different selection procedures that probably fixed different genes. This also was shown by the highly significant mean squares obtained among populations for all the measured traits. The variability among S_1 lines for each population was significant, indicating that variability existed within each population to permit effective selection.

Comparisons between populations (i.e., P_1 vs $P_2 + P_3 + P_4$, P_2 vs $P_3 + P_4$, and P_3 vs P_4) resulted in significant ($P \leq 0.01$ or $P \leq 0.05$) mean squares for most traits. Nonsignificant mean squares occurred for stalk lodging when lines derived from the parental population (P_1) were compared to those from selected populations ($P_2 + P_3 + P_4$). Hence, for stalk lodging, the selected populations responded similarly to the original population. The mass selected population (P_2), however, differed from half-sib and S_1 selected populations for stalk lodging, whereas no difference existed between half-sib (P_3) and S_1 (P_4) selected populations for stalk lodging and ears per plant.

Except for ears per plant and silking date, lines x

environment interactions mean squares were highly significant for all traits. Partition of lines x environment interactions sum of squares into population x environment components resulted in divergent results. For grain yield, only P_3 x environment interaction mean square was found to be not different from zero. The half-sib selected population (P_3) was the only population showing significant interaction mean squares for ear height and grain moisture. Highly significant population x environment interaction mean square was obtained for silking date for the original population (P_1) and for stalk lodging for the mass selected (P_2) population. Root lodging for the S_1 (P_4) selected population had a nonsignificant population x environment mean square.

Although some interactions were significant, the magnitude of the variance component estimates for lines or populations was usually greater than their corresponding estimates of interactions with the environment (Table 18). The results suggested that the relative ranking of lines for each population was (or nearly) the same in each experiment.

One of the objectives of this portion of my study was to determine the effects of mass selection on genetic variability as compared to two other recurrent selection methods. Estimates of variance components, heritability, and genetic coefficients of variation were obtained from the combined analyses of variance, and they are summarized in Table 18.

Table 18. Estimates of phenotypic (σ^2_{ph}), genotypic (σ^2_P), genotypic x environment (σ^2_{PE}), and error (σ^2) variances, heritabilities (h^2), and genetic coefficient of variation (GCV) for the measured traits in each population of S_1 lines combined over four environments

Trait	Populations	$\hat{\sigma}^2_{ph}$	$\hat{\sigma}^2_P$
Grain yield	Krug CO (P_1)	74.99	62.50 ± 11.11
	Krug M (P_2)	77.51	65.50 ± 11.48
	Krug HI (P_3)	57.83	52.91 ± 8.54
	Krug S (P_4)	40.57	27.99 ± 6.08
Root lodging	Krug CO (P_1)	9.25	6.57 ± 1.39
	Krug M (P_2)	7.66	4.85 ± 1.17
	Krug HI (P_3)	11.63	9.28 ± 1.73
	Krug S (P_4)	2.99	2.21 ± 0.45
Stalk lodging	Krug CO (P_1)	4.15	2.59 ± 0.63
	Krug M (P_2)	7.49	4.70 ± 1.14
	Krug HI (P_3)	2.37	1.14 ± 0.37
	Krug S (P_4)	3.61	1.82 ± 0.57
Ear height	Krug CO (P_1)	140.47	128.26 ± 20.79
	Krug M (P_2)	221.66	206.05 ± 32.76
	Krug HI (P_3)	93.55	44.32 ± 15.59
	Krug S (P_4)	101.83	92.85 ± 15.07

$\hat{\sigma}^2_{PE}$	$\hat{\sigma}^2$	h^2 (%)	GCV (%)
10.79 ± 4.72	78.3 ± 2.80	83	27.17
8.90 ± 4.75	78.3 ± 2.80	84	29.86
-19.48 ± 2.60	78.3 ± 2.80	91	15.34
11.15 ± 4.75	78.3 ± 2.80	69	10.69
1.51 ± 0.92	13.03 ± 0.54	71	19.37
1.90 ± 0.96	13.03 ± 0.54	63	17.10
0.55 ± 0.83	13.03 ± 0.54	80	27.67
-1.75 ± 0.55	8.18 ± 0.70	74	17.89
0.98 ± 0.74	7.40 ± 0.78	62	15.30
3.64 ± 0.92	9.46 ± 0.39	63	18.19
0.61 ± 0.60	6.16 ± 0.65	48	11.27
0.66 ± 0.63	9.46 ± 0.39	50	13.11
1.46 ± 4.95	45.90 ± 4.81	91	10.09
4.78 ± 4.98	52.92 ± 2.68	93	8.64
2.02 ± 14.64	52.92 ± 2.68	47	7.02
-0.73 ± 3.83	37.37 ± 3.92	91	10.08

Table 18. (Continued)

Trait	Populations	$\hat{\sigma}^2_{ph}$	$\hat{\sigma}^2_{P}$
Ears/plant	Krug CO (P_1)	0.03	0.03 ± 0.005
	Krug M (P_2)	0.03	0.02 ± 0.004
	Krug HI (P_3)	0.01	0.01 ± 0.002
	Krug S (P_4)	0.02	0.01 ± 0.002
Silk date	Krug CO (P_1)	19.81	16.61 ± 2.96
	Krug M (P_2)	11.76	9.52 ± 1.77
	Krug HI (P_3)	7.59	6.45 ± 1.13
	Krug S (P_4)	6.04	4.93 ± 0.91
Moisture	Krug CO (P_1)	1.05	0.69 ± 0.16
	Krug M (P_2)	2.21	1.71 ± 0.33
	Krug HI (P_3)	1.66	1.07 ± 0.26
	Krug S (P_4)	1.00	0.65 ± 0.16

$\hat{\sigma}^2_{PE}$	$\hat{\sigma}^2$	h^2 (%)	GCV (%)
0.00 ± 0.002	0.03 ± 0.002	77	26.65
0.00 ± 0.002	0.03 ± 0.002	73	23.96
0.003± 0.002	0.02 ± 0.002	60	10.87
0.00 ± 0.002	0.03 ± 0.002	50	10.75
2.81 ± 0.98	7.18 ± 0.36	84	15.18
0.89 ± 0.71	7.18 ± 0.36	81	9.30
0.17 ± 0.46	4.20 ± 0.44	85	11.75
0.32 ± 0.43	3.79 ± 0.40	82	11.01
0.03 ± 0.14	1.37 ± 0.14	66	4.93
0.27 ± 0.15	1.44 ± 0.07	78	7.19
0.46 ± 0.18	1.44 ± 0.07	64	5.59
0.24 ± 0.12	0.93 ± 0.10	65	4.60

For all traits and for each population, the estimates of genetic variance (σ_P^2) were positive and exceeded twice the value of their respective standard errors. Therefore, they are considered to be significantly different from zero. Comparisons between populations can be achieved by relating the difference between their estimated genetic variance to the sum of their respective standard errors. Two estimates were judged to be significantly different from each other when the difference exceeded the sum of their respective standard errors. For grain yield, for example, no significant difference in σ_P^2 was detected between the original, mass, and half-sib selected populations. The estimate of σ_P^2 for S_1 selected population, however, was significantly different from the other three populations, and the magnitude of variance components estimates indicated a substantial decrease in genetic variability for the S_1 selected population. The reduction of σ_P^2 for the S_1 selected population for grain yield was further shown by the relatively lower heritability and reduced genetic coefficient of variability (GCV) estimates (Table 18), as compared to the estimates of the three other populations; a similar trend was observed for root lodging. For ear height, however, the S_1 selected population had greater genetic variability than the half-sib selected population. In most instances, however, S_1 and half-sib derived populations responded similarly

(stalk lodging, ears per plant, silking date, and grain moisture). For some traits, reduced GCV and low h^2 estimates were agronomically advantageous because they indicated that uniformity among lines of these populations was being attained as a result of indirect selection. Consequently, direct selection for those traits will produce very limited progress. Ears per plant was an example that illustrated a favorable decreased genetic variability and heritability values for half-sib and S_1 derived populations while ear height showed the same trend, but only for half-sib derived population.

Estimates of genotypic x environment interaction variances (σ^2_{PE}) were smaller compared to their corresponding genotypic variance (σ^2_P) components for all traits. Most estimates of σ^2_{PE} were not significantly different from zero. Significant σ^2_{PE} estimates were detected for grain yield (except for P_2), root lodging (P_4), and grain moisture (P_3 and P_4). Although significant, these estimates were smaller than their respective estimates of σ^2_P, indicating that the confounding effects of the environments were of minor importance. Negative σ^2_{PE} estimates were obtained for grain yield (P_3), root lodging (P_4), and ear height (P_4). As indicated by Searle (1971), these negative estimates can be considered as evidence that the true value of the component was zero. Several σ^2_{PE} estimates were found to be the same over all

populations. Exceptions were for P_3 for grain yield and ear height that showed relatively lower and higher estimates of σ^2_{PE}, respectively, in comparison with other populations. Estimates of σ^2_{PE} for stalk lodging for P_2 differed from other populations, and P_1 had a higher σ^2_{PE} estimate for silking date. For grain moisture, P_1 and P_3 were the two populations that differed with respect to σ^2_{PE} estimates.

Estimates of heritability are useful for designing selection plans and for predicting expected progress from selection for a given trait in the population. Heritability estimates (Table 18) were generally high for all traits, indicating that selection for these traits will be effective. Relative to other populations, moderately lower h^2 values were observed for P_4 (grain yield), P_2 (root lodging), P_3 and P_4 (stalk lodging and ears per plant), P_3 (ear height), and P_1 and P_4 (grain moisture). Hence, for these traits, progress from selection in the reference population will be slower in comparison to other populations, particularly if a simpler selection scheme, such as mass selection, was applied.

Phenotypic correlation coefficients (r_{ph}) computed from the combined data among seven traits observed for each population are presented in Table 19. These r_{ph} values can be regarded as estimates of genotypic correlation coefficients (r_g) since the environmental bias was reduced by

Table 19. Phenotypic correlation coefficients (r_{ph}) among traits for each population combined over four environments

Traits	Populations	Traits					
		Stalk lodging	Ear height	Silk date	Ears/ plant	Moisture	Grain yield
Root lodging	CO (P_1)	-0.27**	0.45**	0.32**	-0.10	0.32**	-0.11
	M (P_2)	0.11	0.39**	-0.02	-0.04	0.09	-0.05
	HI (P_3)	-0.04	0.35**	0.14	-0.01	0.22*	-0.01
	S (P_4)	0.29**	0.46**	0.17	-0.02	0.07	0.18
Stalk lodging	CO (P_1)		-0.11	-0.36**	0.30**	-0.25*	0.20*
	M (P_2)		0.22*	-0.09	0.18	-0.10	0.31**
	HI (P_3)		-0.15	-0.16	-0.01	-0.10	-0.21*
	S (P_4)		0.23*	-0.02	-0.07	0.09	0.27**
Ear height	CO (P_1)			0.36**	-0.15	0.33**	-0.16
	M (P_2)			0.28**	0.03	0.00	-0.07
	HI (P_3)			0.15	0.16	0.13	0.38**
	S (P_4)			0.10	0.07	0.13	0.25*

Silk date	CO (P_1)	-0.74**	0.19	-0.72**
	M (P_2)	-0.63**	0.22*	-0.71**
	HI (P_3)	-0.50**	0.37**	-0.36**
	S (P_4)	-0.26**	0.32**	-0.18
Ears/ plant	CO (P_1)		-0.11	0.83**
	M (P_2)		-0.25*	0.81**
	HI (P_3)		-0.14	0.57**
	S (P_4)		-0.10	0.48**
Moisture	CO (P_1)			0.02
	M (P_2)			-0.16
	HI (P_3)			0.01
	S (P_4)			0.04

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

measuring each trait in several environments. Lantin (1980) computed r_{ph} and r_g estimates from the combined data recorded over several environments and found that both coefficients were about equal for all pairs of traits.

Generally, low r_{ph} estimates were obtained for several pairs of traits. Although some of these low associations proved to be statistically significant ($P \leq 0.01$ or $P \leq 0.05$), they were of limited usefulness because their corresponding coefficients of determinations (R^2) were very low. Grain yield was significantly ($P \leq 0.01$) correlated with ears per plant in each population. The magnitude of r_{ph} values, however, was greater for the original ($r_{ph} = 0.83$) and the mass selected populations ($r_{ph} = 0.81$) than for half-sib ($r_{ph} = 0.57$) and S_1 ($r_{ph} = 0.48$) selected populations. Negative correlations, varying from -0.72 for the original and -0.71 for mass selected populations to -0.36 for the half-sib population, were obtained between grain yield and silking date, but the r_{ph} value was low (-0.18) and not significant for S_1 selected population. These associations indicated that grain yield enhancement in these populations can be achieved through selection for earliness and prolificacy, particularly in the original and mass selection populations that had higher r_{ph} values. The importance of these two traits was further shown by highly significant, but negative, r_{ph} estimates obtained between silking date and ears per

plant, suggesting that silking emergence was hastened on prolific plants. The r_{ph} estimates were higher for the original and mass selected populations (r_{ph} = -0.37 and -0.63, respectively) than for the half-sib (r_{ph} = -0.50) and S_1 (r_{ph} = -0.26) selected populations. These negative associations may be caused by lack of pollen for the late maturing plants, resulting in lower seed set and barrenness and, consequently, reduced grain yield.

Significantly positive, but low, correlations were obtained between grain yield and stalk lodging, except for half-sib selection where a negative r_{ph} was observed. Low r_{ph} estimates also were obtained between grain yield and ear height for half-sib (r_{ph} = 0.38) and S_1 (r_{ph} = 0.25) selected populations. These estimates suggested that higher yielding genotypes were susceptible to stalk breakage (except for the half-sib selected population). For the half-sib and S_1 selected populations, genotypes with higher ear position were higher yielding. This is conceivable because numerous studies have shown strong positive associations between plant height and ear height. Thus, plants with low ear position were shorter and, consequently, affected by shading from taller plants.

In addition to grain yield, significant moderate to low r_{ph} estimates were obtained between other traits. Root lodging was positively and moderately correlated ($P \leq 0.01$)

with ear height. Obviously, susceptibility to lodging increases with ear height. Low and significant r_{ph} values were observed between stalk lodging and ear height for the mass and S_1 selected populations. Silking date showed significant associations with grain moisture for the selected populations. This is understandable because the later maturing genotypes were expected to contain higher grain moisture at harvest. Silk date was also significantly correlated with ear height for the original and the mass selected populations; both populations were taller than the S_1 and half-sib selected populations (Table 16). Hence, the photosynthate produced in these two populations seemingly was used in the development of taller plants with high ear position instead of being used in the formation and development of kernel primordia.

Some of the correlated responses to selection for grain yield in the four populations are graphically illustrated in Figures 6 to 9. Table 20 summarizes means, standard deviations of means, and ranges observed for each trait from the combined data. S_1 lines derived from mass selected population were 6.85% lower yielding, whereas S_1 lines derived from the half-sib and S_1 selected populations were 63% and 70%, respectively, greater yielding than the original population (Figure 6). Decreased grain yield for the S_1 lines derived from the mass selected population could be attributed

Figure 6. Frequency distributions of grain yield of 100 S_1 lines of the original (P_1) and selected (P_2, P_3, P_4) Krug(BSK) populations

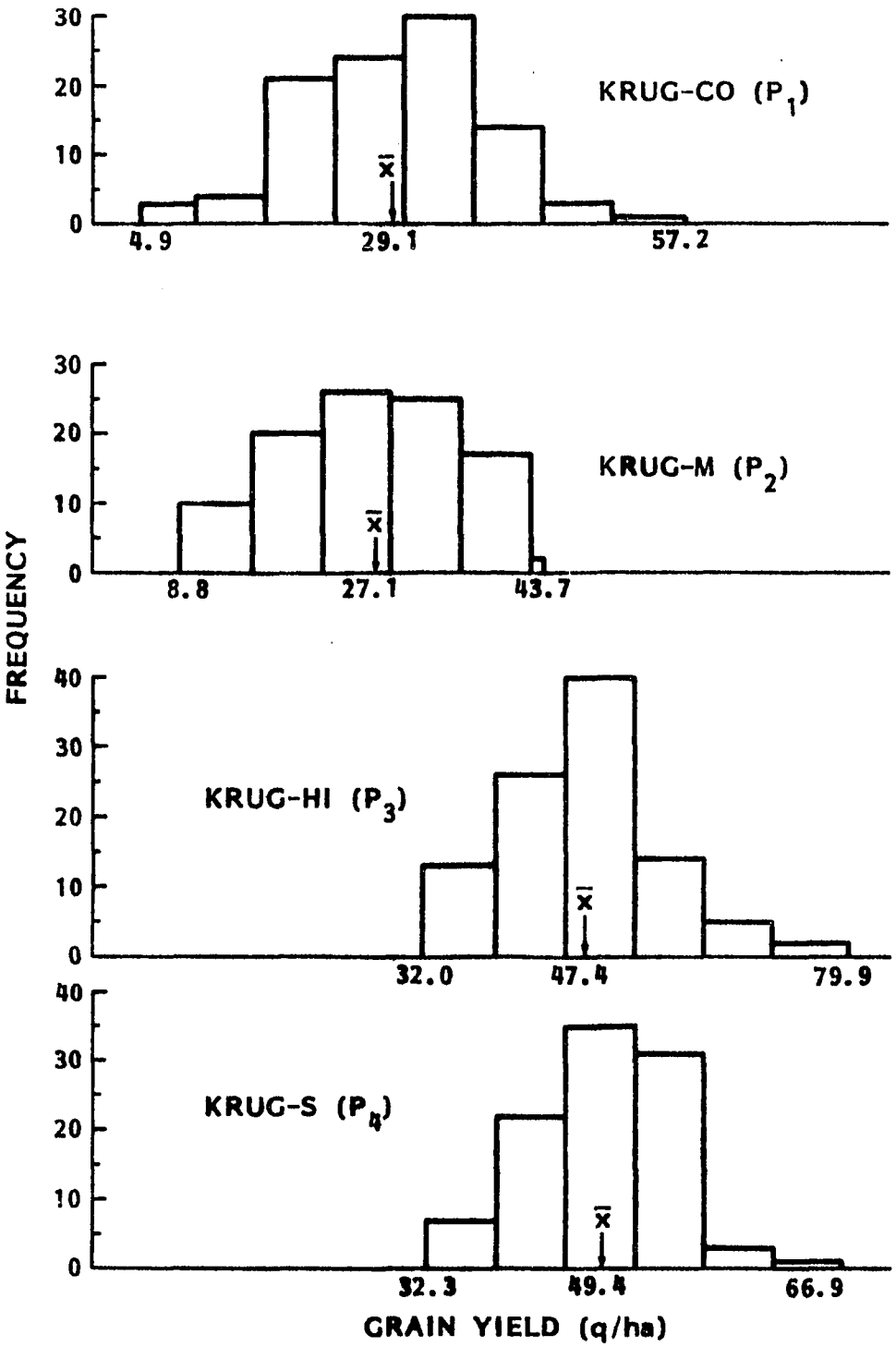
KRUG-CO (P_1)
KRUG-M (P_2)
KRUG-HI (P_3)
KRUG-S (P_4)
$\bar{x}$
4.9
29.1
57.2
8.8
27.1
43.7
32.0
47.4
79.9
32.3
49.4
66.9
FREQUENCY
GRAIN YIELD (q/ha)

Figure 7. Frequency distributions of ears per plants of 100 S_1 lines of the original (P_1) and selected (P_2, P_3, and P_4) Krug(BSK) populations

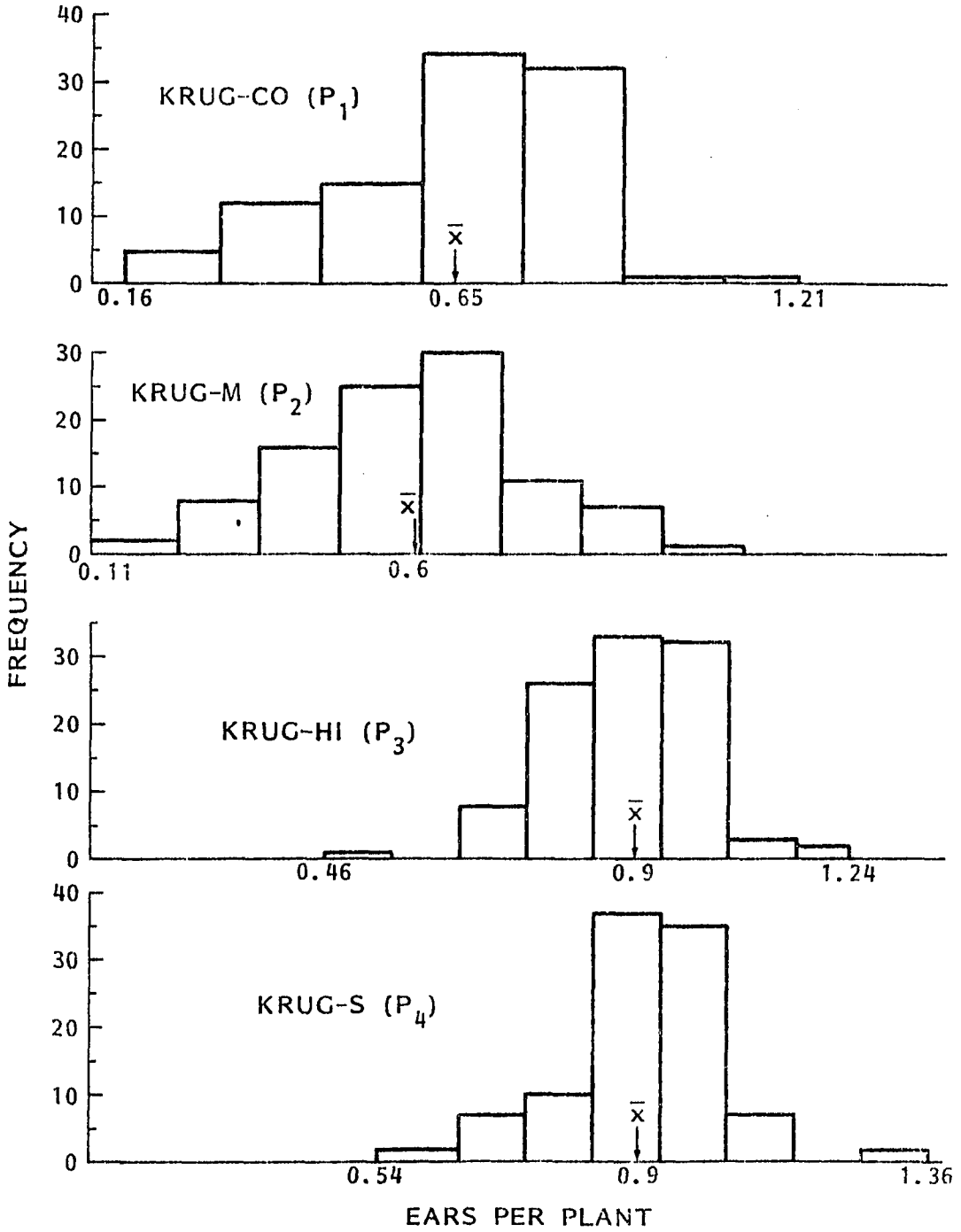
KRUG-CO (P_1)
KRUG-M (P_2)
KRUG-HI (P_3)
KRUG-S (P_4)
$\bar{x}$
0.16
0.65
1.21
0.11
0.6
0.46
0.9
1.24
0.54
0.9
1.36
0
10
20
30
40
FREQUENCY
EARS PER PLANT

Figure 8. Frequency distributions of silking date of 100 S_1 lines of the original (P_1) and selected (P_2, P_3, and P_4) Krug(BSK) populations

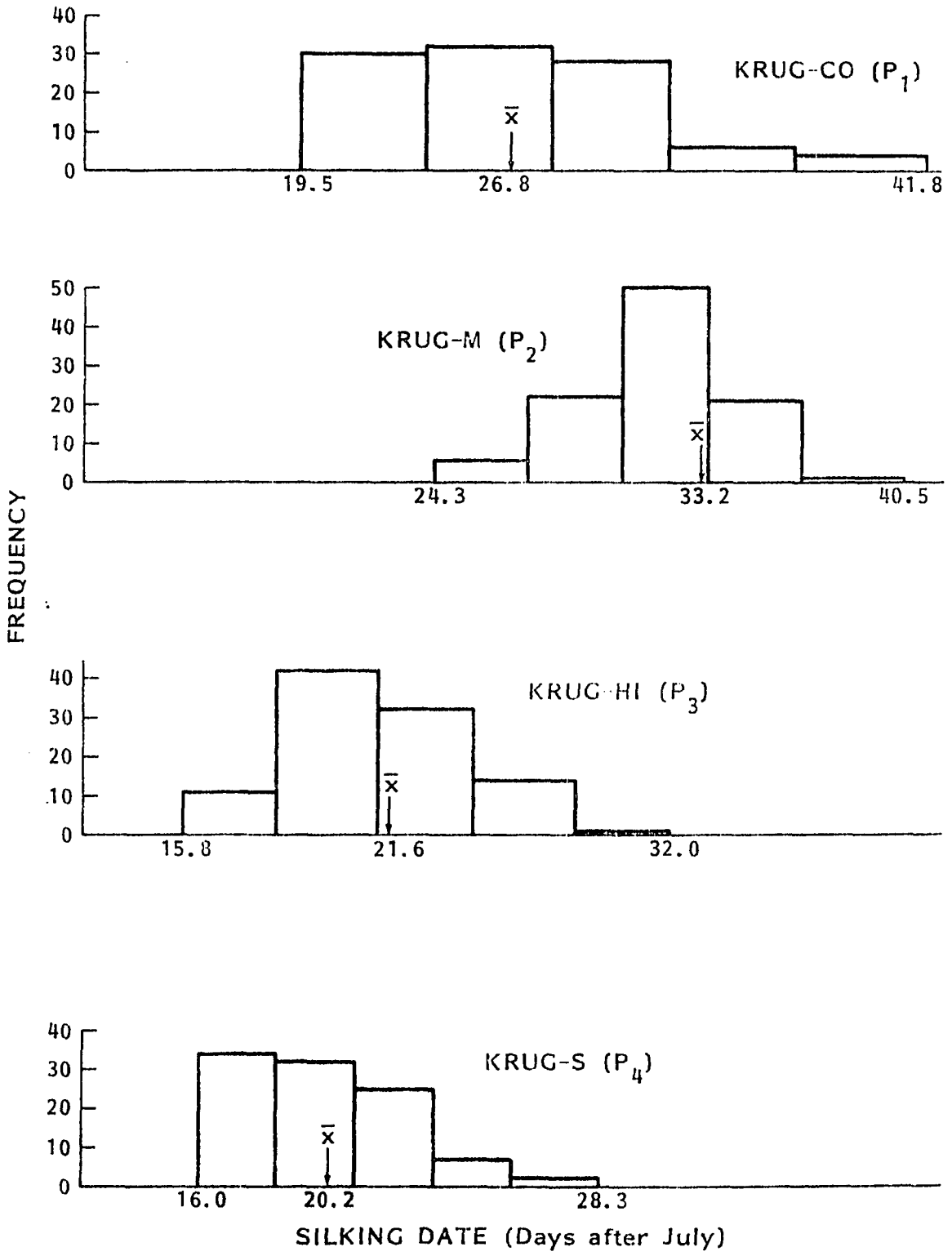
KRUG-CO (P_1)
KRUG-M (P_2)
KRUG-HI (P_3)
KRUG-S (P_4)
$\bar{x}$
19.5
26.8
41.8
24.3
33.2
40.5
15.8
21.6
32.0
16.0
20.2
28.3
FREQUENCY
SILKING DATE (Days after July)

Figure 9. Frequency distributions of ear height of 100 S_1 lines of the original (P_1) and selected (P_2, P_3, and P_4) Krug(BSK) populations

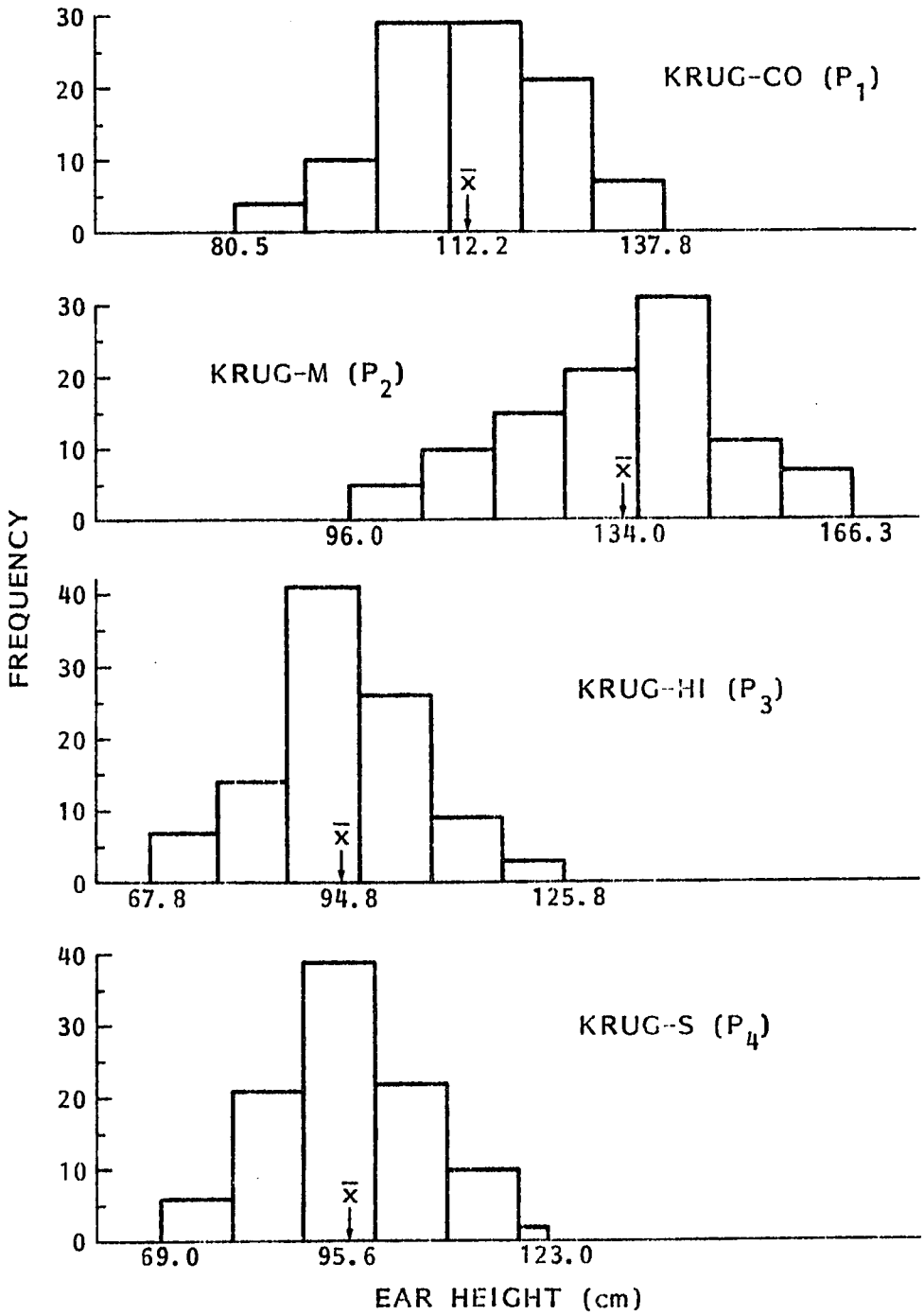
KRUG-CO (P_1)
KRUG-M (P_2)
KRUG-HI (P_3)
KRUG-S (P_4)
FREQUENCY
EAR HEIGHT (cm)
80.5
112.2
137.8
96.0
134.0
166.3
67.8
94.8
125.8
69.0
95.6
123.0

Table 20. Means, standard deviation of means ($S_{\bar{X}}$), and ranges of seven traits measured on 100 S_1 lines of each population combined across several environments

Trait	Population	Mean	$S_{\bar{X}}$	% of CO	Range
Yield (q/ha)	CO (P_1)	29.07	±6.03	100.00	4.89-57.16
	M (P_2)	27.08	±5.79	93.15	8.82-43.73
	HI (P_3)	47.38	±5.31	162.99	31.98-79.90
	S (P_4)	49.43	±4.55	170.04	32.30-66.93
Moisture (%)	CO (P_1)	16.85	±1.14	100.00	14.30-19.75
	M (P_2)	18.19	±1.60	107.95	15.40-22.15
	HI (P_3)	18.51	±1.27	109.85	15.75-21.10
	S (P_4)	17.54	±1.14	104.09	15.07-21.38
Ears/ plant	CO (P_1)	0.65	±0.18	100,00	0.16-1.21
	M (P_2)	0.59	±0.17	90.77	0.11-1.08
	HI (P_3)	0.92	±0.11	141.44	0.46-1.24
	S (P_4)	0.93	±0.12	143.08	0.54-1.36
Silk date	CO (P_1)	26.84	±4.48	100.00	19.50-41.75
	M (P_2)	33.18	±3.45	123.62	24.25-40.50
	HI (P_3)	21.61	±2.85	80.51	15.75-32.00
	S (P_4)	20.17	±2.50	75.15	16.00-28.25
Ear height	CO (P_1)	112.22	±11.69	100.00	80.50-137.75
	M (P_2)	134.02	±15.62	119.43	96.00-166.25
	HI (P_3)	94.81	±11.17	84.49	67.75-125.75
	S (P_4)	95.57	±10.30	85.16	69.00-123.00
Root lodging	CO (P_1)	13.23	±3.32	100.00	7.25-19.99
	M (P_2)	12.88	±3.09	97.35	7.22-21.61
	HI (P_3)	11.01	±3.62	83.22	6.29-22.90
	S (P_4)	8.31	±1.75	62.82	5.88-13.92

Table 20. (Continued)

Trait	Population	Mean	$S_{\bar{X}}$	% of C0	Range
Stalk lodging	C0 (P_1)	10.52	±2.06	100.00	6.37-16.79
	M (P_2)	11.92	±2.81	113.31	6.22-23.08
	HI (P_3)	9.47	±1.58	90.02	6.00-13.65
	S (P_4)	10.29	±1.96	97.81	6.79-16.17

to the expression of deleterious recessive genes due to inbreeding. Nonsignificant changes over cycles were observed when mass selection program was evaluated using B73 as tester. It is hypothesized that the Krug population possesses many deleterious genes that govern most traits. This hypothesis seems to be confirmed because one generation of selfing in the 14th cycle of mass selection exposed the recessive genes that, consequently, reduced grain yield. The yield reduction of the S_1 lines derived from the mass selected population also was accompanied by a 9.2% reduction in number of ears per plant (Figure 7), delayed silking date of 23.6% (Figure 8), and increased ear height of 19.4% (Figure 9), as compared to the S_1 lines derived from the original population. Conversely, S_1 lines from half-sib and S_1 selected populations had yield increases that were associated with 41.4 and 43.1% increased ears per plant, reduced silking date of 19.5 and 24.9%, and reduced ear height of 15.5 and 14.8%, respectively.

Another negative effect of mass selection was a 13.3% increase in stalk breakage while S_1 lines from the half-sib and S_1 selected populations had an average decrease in stalk lodging of 10.0 and 2.2%, respectively. Although a slight decrease of 2.6% was observed for root lodging for S_1 lines from the mass selected population, substantial reductions were observed for stalk lodging for S_1 lines from the half-sib (16.8%) and S_1 (37.2%) selected populations.

Comparisons among the three recurrent selection methods were performed by computing the expected genetic gains for each trait (Table 21). Because the three selection methods differed in number of seasons or years required to complete each cycle, expected genetic gain was expressed on a per year basis to give a common basis for comparison. Using the prediction formulae for genetic gain proposed by Eberhart (1970) and extended by Empig et al. (1972), the expected genetic gains per year were computed as follows:

Mass selection: $$\frac{k \cdot (\frac{1}{2})\sigma_A^2}{y\sqrt{\sigma_w^2 + \sigma^2 + \sigma_{PE}^2 + \sigma_P^2}}, \quad y = 1;$$

Half-sib: $$\frac{k \cdot (\frac{1}{2})\sigma_A^2}{y\sqrt{\frac{\sigma^2}{re} + \frac{\frac{1}{4}\sigma_{AE}^2}{e} + \frac{1}{4}\sigma_A^2}}, \quad y = 2;$$

and S_1 selection: $$\frac{k \cdot \sigma_A^2}{y\sqrt{\frac{\sigma^2}{re} + \frac{\sigma_{AE}^2}{e} + \sigma_A^2}}, \quad y = 2.$$

Table 21. Expected genetic gain (ΔG) per year under different intrapopulation selection schemes applied to Krug(BSK) for seven traits

Traits[a]	Mass selection			Half-sib selection			S_1 selection		
	ΔG	Obs.	% of predicted	ΔG	Obs.	% of predicted	ΔG	Obs.	% of predicted
Grain yield (q/ha)	1.79	-0.14	7.82	3.60	1.14	31.67	8.59	1.27	14.78
Root lodging (%)	-0.47	-0.03	6.38	-0.84	-0.14	16.66	-3.32	-0.31	9.34
Stalk lodging (%)	-0.21	0.10	47.62	-0.73	-0.06	8.22	-1.25	-0.01	0.80
Ear height (cm)	-3.98	1.56	39.20	-11.60	-1.71	14.74	-22.24	-1.67	7.51
Ears/ plant (no.)	0.04	-0.004	10.00	0.10	0.017	17.00	0.38	0.0175	4.61
Silk date (days)	-1.54	0.45	29.22	-2.64	-0.33	12.50	-5.92	-0.42	7.09
Moisture (%)	-0.14	0.10	71.43	-0.23	0.10	43.48	-0.60	0.04	6.67

[a]Comparisons between predicted and observed gains are not really valid for traits other than grain yield because the observed values are correlated responses of selection rather than direct responses.

The number of years required to complete each cycle of half-sib or S_1 selections assumed that winter nurseries were available for either isolation of genotypes (topcrossing or selfing) or recombination of selected genotypes. The selection intensity used in each selection method was 10% (i.e., k = 1.75). Use of the foregoing formula for mass selection was not entirely correct because data were collected on a per plot basis, and not on an individual plant basis. Hence, estimates of σ_w^2 were not available. Robinson et al. (1949), however, showed that σ^2 was relatively small compared to σ_w^2. Gardner (1961) encountered similar difficulty and simply assumed that σ_w^2 was 10 times greater than σ^2 to predict the genetic gain from his mass selection program. Therefore, the same ratio ($\sigma_w^2/\sigma^2 = 10$) was used to predict the expected genetic gain from mass selection presented in Table 21.

Results suggested that greater genetic gains were expected from S_1 selection for all traits. This was expected because S_1 selection uses all the additive variances while mass selection and half-sib (with selfed seeds recombined) use only ½ of additive variances. Moreover, the masking effect of tester used in half-sib selection and lack of parental control for mass selection render these two selection schemes to be less effective. These results corroborate those reported by Burton et al. (1971) who compared half-sib

and S_1 progeny testing procedures after four cycles, and by Genter (1973). For all traits, half-sib selection was superior to mass selection. In all instances, the predicted gains exceeded the observed gains.

DISCUSSION

Estimates of progress from mass selection for grain yield in the Krug(BSK) population were considerably lower than those reported by other investigators who used similar selection schemes. After 14 cycles, the gains per cycle were only 0.80% and 0.56% (from means of seven and nine locations, respectively) for the populations per se, and 0.85% gain per cycle (from means of seven locations), for populations x CO. Although the coefficients of regression were significant, they were smaller in comparison to the nonsignificant regression coefficient of 0.76 reported by Hallauer and Sears (1969) who made an evaluation after six cycles of mass selection. The significance of the observed changes from cycle to cycle after 14 cycles could be attributed to extensive testing conducted at seven and nine locations in three different years. Insufficient testing was hypothesized as one of the possible reasons for the limited progress observed after six cycles; Hallauer and Sears (1969) used sequential testing, and the later cycles were not tested as extensively as the earlier cycles. Conversely, all cycles of selection were equally tested in my study. Significant regression coefficients were obtained from increased number of locations while replication number did not have any effect (Table 8). Eberhart (1972) suggested that allocation of resources to conduct yield trials with two replications in each of four

locations was superior to four replications in two locations.

Although the rates of gain per cycle in my study seemed low, they do not differ from those reported by Mareck and Gardner (1979); they reported gains of 0.80 to 0.90% per cycle, when they evaluated the C0 and C15 populations over a wide range of Nebraskan environments. Similar results were previously reported by Genter and Eberhart (1974) after extensive yield tests of the C0 and C12 populations obtained from Gardner's mass selection program for increased grain yield. Arboleda-Rivera and Compton (1974) also obtained significant yield improvement from their mass selection program when the selected populations were yield tested under conditions similar to those of selection. Decreased yield was observed when testing was conducted under unfavorable conditions. Hence, it seems that the advantage of mass selection, i.e., elimination of expensive and time consuming yield trials, has the disadvantage of selecting populations that are environment-specific. This hypothesis is also supported by significant mean squares observed for grain yield measured at Ames Agronomy Research Center for populations per se in 1978 and populations x C0 in 1979 (Tables 3 and 7 in the Appendix). If this limitation of mass selection is general, breeders would have to conduct several mass selection programs concurrently to attain their goal of developing broadly adapted populations, or the concept of

convergent-divergent selection proposed by Lonnquist et al. (1979); but the advantages attributed to mass selection, therefore, would be nullified.

Lack of substantial genetic variability in the Krug(BSK) population also could be an explanation for the limited response to mass selection for grain yield. The Krug(BSK) population was synthesized from only eight S_1 lines on the basis of their topcross performance. A highly selected number of lines could contribute to a narrower genetic basis in comparison to other maize populations that have responded favorably to mass selection for grain yield. Hallauer and Miranda (1981) summarized the estimates of additive genetic variance and heritability values for grain yield from 99 different studies, including five different types of maize populations. Synthetic varieties, such as Krug, had the lowest estimates of genetic variability in comparison to the composite, F_2, open-pollinated, and variety cross populations. This ranking of the different populations suggests that Krug(BSK), which is a synthetic variety, may have had less genetic variability than other populations before mass selection was initiated.

The plant density used for mass selection could have been another factor that limited progress obtained from mass selection in the Krug(BSK) population. Gardner (1961) used a population density of about 19,700 plants per hectare

in his nurseries whereas the isolation fields for Krug included nearly 39,000 plants per hectare. Lonnquist (1967) and Prior and Russell (1975) observed that at lower plant densities, selection for prolificacy was more effective; selected genotypes tended to produce at least one ear when grown at higher population densities and had reduced frequency of barrenness. Harris et al. (1972) suggested that selection of single-eared plants may inhibit the expression of genes controlling yield in a population. Torregroza and Harpstead (1967), for example, harvested more grain yield (28%) from selection for prolificacy whereas selection for single-eared plants decreased grain yield by 5% in comparison with the original population. The correlation coefficient (r_{ph}) between grain yield and ears per plant and the correlated response of ears per plant to selection for grain yield suggested that prolificacy was important for higher yield (Figures 2 and 7). In my study, the adoption of higher plant density for selection was justified by commercial needs and simulation of farmer's condition is essential for the release and acceptance of any variety. Use of lower plant densities for selection is questionable since Mareck and Gardner (1979) obtained a reduced response to selection when they tested the C0 and C15 at higher plant densities.

Hallauer and Sears (1969) hypothesized that exclusion of stalk-lodged plants from selection could explain partially

the limited progress realized from their evaluation. Although a nonsignificant correlation between grain yield and stalk lodging was obtained from their study, my study showed a positive r_{ph} (0.31**) between grain yield and stalk lodging (Table 19). Each cycle of mass selection for grain yield also increased stalk lodging (Figure 5). Because the stalk-lodged plants were excluded from selection in each sub-block, it was assumed that selection intensity was reduced. Based on results shown in Table 21, exclusion of stalk-lodged plants relaxed selection pressure from 7.5% to about 27.4% for populations per se; this reduction in selection pressure would reduce the effectiveness of selection for greater grain yield. The exclusion of stalk-lodged plants could possibly have eliminated some of the highest yielding genotypes. Selection of stalk-lodged plants is agronomically unacceptable because it increases the incidence of ear rot and damage due to rodents, which also limited grain yield Higher incidence of stalk lodging also reduced grain yield if mechanical harvesting is used and increases labor costs if unharvested ears are manually gleaned.

Limited progress from mass selection for grain yield observed in the Krug(BSK) population could be attributed to one or combination of the following causes: (1) reduced amount of genetic variability that was present in the population before mass selection was initiated; (2) inef-

fective selection resulting from selection performed at higher population density which inhibited the expression of higher yielding genotypes; (3) lack of response when evaluations were extended beyond the selection site; and (4) exclusion of stalk-lodged plants which reduced the intensity of selection and eliminated higher yielding genotypes in the basic selection units.

The effect of mass selection on the genetic variability was assessed by comparing the estimates of components of variance of unselected S_1 lines (σ_P^2) from the original (P_1) and the selected populations (P_2, P_3, and P_4). The estimated components of genetic variance (σ_P^2) were translated into estimates of additive genetic variances (σ_A^2) under the assumptions of no dominance, in which case $\sigma_P^2 = \sigma_A^2$; or if gene frequencies were equal for all loci (i.e., $p = q = 0.5$), then $\sigma_P^2 = \sigma_A^2 + \frac{1}{4}\sigma_D^2$, assuming no epistasis.

The assumption of no dominance was valid if homozygous inbred lines ($F = 1$) were evaluated. With each generation of inbreeding, the additive variance increases and dominance variance decreases until at complete homozygosity, the lines include twice the initial amount of additive variance and no dominance. Lines included in my study were selfed only one generation and represented random S_0 plants. Hence, $F = 0$ and at that level of inbreeding, bias due to dominance could lead to an overestimation of additive variance.

Lindsey et al. (1962) applied the nested genetic design (DI) to study the nature of gene action present in the Krug Yellow Dent population. They reported large amount of additive variance for all traits in one year. In the second year, however, they observed a reduction of additive variance. They implicated assortative mating to be the cause of the observed differences between estimates of the two years. The design imposed in the development of progenies evaluated in my study did not involve matings between parents. There was no intentional selection in developing the S_1 lines, and the sample size used for each population (100 S_1 lines) was judged to be adequate. Hence, the requirements of randomness and sample size were assumed to be valid.

Estimates of genetic components of variance in the Krug (BSK) population also were studied by Wright et al. (1971). Using the diallel mating design, they found that for all traits, additive variance accounted for most of the total genetic variance, but both estimates (σ_A^2 and σ_D^2) were significantly different from zero. These results indicated that the assumption of no dominance in Krug(BSK) population may not be valid. However, the bias due to dominance variance would be small because additive variances were larger than dominance variances for all traits. Results from triallel analyses conducted by Wright et al. (1971) showed that sig-

nificant amounts of epistatic effect were present in Krug (BSK) for all traits, but additive epistatic effects were more important than dominance epistatic effects. Although the existence of epistatic effects were detected in the Krug(BSK), the bias on the assumption of no epistasis was negligible because the additive epistatic effects were greater than the dominance effects, and the additive epistatic effects were fixable through selection.

Cyclical selection that characterizes recurrent selection is possible only if the amount of genetic variability in the population is maintained over cycles. Results obtained in my study indicated that this requirement was met for the mass selected and the half-sib derived populations, suggesting that effective selection in future cycles of selection would be possible. For S_1 derived population, however, a decrease in genetic variability was evident, suggesting that response from future cycles of selection may be reduced. Reduced genetic variability observed for S_1 recurrent selection could be caused by effective testing procedures that excluded genotypes with deleterious recessive alleles because of selfing. Selection against deleterious alleles would not be as effective for mass or half-sib selection because random matings and testers, respectively, masked the undesirable alleles. Hence, effective identification of genotypes with high performance resulted in accumula-

tion of favorable genes after eight cycles of S_1 recurrent selection and, consequently, decreased genetic variability. Inbreeding because of the selection intensity used (k = 1.75 or 10 lines recombined for each cycle) cannot be the only cause for the reduction in genetic variability observed for S_1 progeny selection because similar selection pressure was used for half-sib selection. There was no evidence of reduced genetic variability with half-sib recurrent selection after eight cycles of selection.

Hallauer and Miranda (1981) summarized the estimates of variance components and genetic coefficient of variability (GCV) obtained for grain yield after each cycle of half-sib and S_1 selection conducted in the Krug(BSK) population. Their estimates were converted to grams per plant to obtain a common basis for comparison while those determined in my study were expressed in quintals per hectare. The GCVs, however, were computed as the genetic standard deviation expressed as percentage of the means and, thus, provide a common basis for comparisons. For half-sib selection, under the assumptions of p = q and no epistasis, the GCV observed after the eighth cycle was equivalent to 5.1; I evaluated S_1 lines that are equal to $\sigma_P^2 = \sigma_A^2 + \frac{1}{4}\sigma_D^2$ and the corresponding GCV was 15.3. Hallauer and Miranda (1981) evaluated half-sib progenies (i.e., $\frac{1}{4}\sigma_A^2$) and reported a GCV equal to 5.0. Hence, genetic variability was maintained

over cycles with half-sib selection. For S_1 progeny selection, however, the GCV decreased from 17.6 to 3.6 when comparing the seventh and the eighth cycles of selection.

Comparisons between the three recurrent selection schemes showed that S_1 selection was superior to other methods for improving and predicting genetic gains from selection for most traits (Table 21). These results were in agreement with those reported by Burton et al. (1971), Genter (1973), and Genter and Alexander (1966). Carangal et al. (1971) and Burton et al. (1971) indicated that improvement of populations *per se* would be achieved more efficiently by S_1 evaluations. Mass selection has the advantage of being simpler, cheaper, and more expedient. However, the effectiveness of mass selection for improving complex traits with low heritability values is questionable, based on the results of my study. S_1 recurrent selection has the advantage of reducing the resources required for the production of testcrosses with half-sib recurrent selection.

Discrepancies between observed and predicted gains under any recurrent selection scheme for all traits suggested that the additive genetic variance was overestimated. The assumptions of no dominance and no epistasis could create bias in overestimating σ_P^2, and consequently, σ_A^2. Another source of bias could result from genotype x environment interaction. Comstock and Moll (1963) indicated that genotype x environment

interaction can be important in causing a bias in the estimates of genetic variance components. They indicated that usually the second-order interaction (genotype x location x year) in maize is greater than the first-order interaction (i.e., either genotype x location or genotype x year). They also emphasized that the bias was important, particularly when the estimates were obtained from a single year at one location. For my study, materials were evaluated in four environments. The estimates of σ^2_{PE} were smaller than those of σ^2_P and, in most instances, they were not significantly different from zero. Some estimates of σ^2_{PE}, however, were significant. Significant estimates of σ^2_{PE} suggested that selection from only one environment (e.g., mass selection) may be confounded by the environmental disturbances.

Reduced genetic variability also could be the cause of the difference between observed and predicted genetic gains. As noted for S_1 progeny selection, genetic variance decreased after the eighth cycle and this may lead to overestimation of predicted genetic gain in successive cycles of selection.

SUMMARY

The objectives of my study were to: (1) evaluate the effectiveness of 14 cycles of mass selection for grain yield in the Krug(BSK) population; (2) determine the effect of three selection procedures on genetic variability; and (3) compare the effectiveness of three selection methods for the improvement of Krug(BSK) S_1 lines for grain yield and other agronomic traits.

Progress from mass selection was determined by evaluating the populations *per se* [original (C0) and the even cycles of selection (C2, C4, ..., C14)] and two sets of testcrosses (Cn x C0 and Cn x B73). These plant materials were grown in nine Iowa locations in 1978, 1979, and 1980. Regression analyses were performed on cycles of selection to obtain the estimates of genetic progress from mass selection. For grain yield, significant positive linear responses were obtained for populations *per se* and populations x C0, but not for populations x B73. Lack of response noted for populations x B73 was due to buffering effects of alleles from the inbred B73. Significant linear trends also were observed for stalk lodging and grain moisture for populations *per se*. Silking date and ear height showed quadratic responses for populations *per se*, and for ear height for populations x C0. For the populations x B73, however, silking date and ear height showed only significant linear

responses. Nonsignificant linear responses were obtained for ears per plant, root lodging, and dropped ears.

Although significant change over cycles was detected for grain yield, the response was considerably lower (about one-half q/ha) compared to those reported by other researchers. Increased yield, however, resulted in lateness, increased stalk breakage, and higher ear position. These undesirable correlated responses were attributed to numerous deleterious genes present in Krug(BSK) population and the criteria used for mass selection (i.e., higher grain yield).

Estimates of genetic variability and comparisons between different selection methods were obtained through evaluation of 400 unselected S_1 lines in four environments in 1980. The 400 S_1 lines represented the original, the 14th cycle of mass selected population, and the eighth cycles of half-sib and S_1 selected populations. Estimates of variance components, heritability values, and predicted genetic gains for each trait in each population were computed. Reduced genetic variability for grain yield was observed for the S_1 selected population, whereas the mass and half-sib derived populations showed no evidence of reduced genetic variance. The mass selected population had increased genetic variability for stalk lodging, ear height, silk date, and grain moisture. For most traits, the half-sib and the S_1 derived populations responded similarly, except for root lodging and

ear height; half-sib and S_1 derived populations had greater genetic variability for root lodging and ear height, respectively. In most instances, heritability estimates were high for all traits.

Correlations between a pair of traits indicated that silking date and ears per plant were the most important traits that limited grain yield, particularly for the original and the mass derived populations. Analyses of the frequency distribution of S_1 lines revealed that the mass selected population was 6.85% lower yielding than S_1 lines from the original population. Reduced yield was because of expression of deleterious genes following selfing. The mass selected population also had delayed silk emergence (23.6%), increased stalk breakage (13.3%), and increased ear height (19.4%). In contrast, the half-sib and the S_1 derived populations had increased yield (63 and 70%), greater number of ears per plant (41 and 43%), reduced ear height (15.5 and 14.9%), and flowered earlier (19.5 and 24.9%), respectively.

Predicted genetic advance from selection indicated that S_1 selection predicted greater genetic gain for all traits. In all cases, predicted genetic gain exceeded the observed gain.

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APPENDIX

Table A1. Analyses of variance for five traits measured on mass selected populations and their testcrosses grown at Nashua in 1978

Source of variation	d.f.	Mean squares				
		Root lodging	Stalk lodging	Ears/ plant	Dropped ears	Grain yield
Rep	2	1.26	0.23	0.013	3.00	6.97
Entry	29	8.86**	4.44**	0.014**	13.78	334.93**
Group 1	1	4.31	3.91	0.007	15.56	13.85
Group 2	6	4.48	4.72	0.007	16.23	12.48
Group 3	7	5.73	14.68**	0.034**	7.22	76.57
Group 4	6	18.71**	7.26*	0.022**	8.14	460.58**
Among groups	3	-	-	-	-	-
Error	58	4.01	2.41	0.007	11.57	62.51
CV (%)		23.25	21.95	8.98	112.34	16.14

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Table A2. Analyses of variance for five traits measured on mass selected populations and their testcrosses grown at Kanawha in 1978

Source of variation	d.f.	Mean squares				
		Root lodging	Stalk lodging	Ears/ plants	Dropped ears	Grain yield
Rep	2	2.66	1.30	0.028	173.93	99.29
Entry	29	3.22	9.81*	0.031**	26.94	338.22**
Group 1	7	6.31	9.62	0.008	12.25	31.86
Group 2	6	1.04	1.56	0.020	10.46	60.11
Group 3	7	1.15	7.42	0.013	8.91	53.57
Group 4	6	5.38	13.44*	0.037**	27.90	525.90**
Among groups	3	-	-	-	-	-
Error	58	5.05	5.46	0.009	25.59	41.79
CV (%)		31.68	21.56	9.69	111.47	11.41

* and ** indicate significance at 5 and 1% levels of probability, respectively.

Table A3. Analyses of variance for three traits measured on mass selected populations and their testcrosses grown at Ames Agronomy Research Center in 1978

Source of variation	d.f.	Mean squares		
		Ears/ plant	Silk date	Grain yield
Rep	2	0.002	6.21	52.58
Entry	29	0.035**	24.04**	514.68**
Group 1	7	0.028**	3.62**	145.81*
Group 2	6	0.009	1.27	37.38
Group 3	7	0.013	0.67	120.18
Group 4	6	0.029**	32.49**	575.74**
Among groups	3	-	-	-
Error	58	0.009	0.68	55.83
CV (%)		10.32	3.35	12.24

* and ** indicate significance at 5 and 1% levels of probability, respectively.

Table A4. Analyses of variance for six traits measured on mass selected populations and their testcrosses grown at the Atomic Energy site in 1978

Source of variation	d.f.	Mean squares					
		Root lodging	Stalk lodging	Ears/ plants	Dropped ears	Silk date	Grain yield
Rep	2	8.62	23.54	0.012	2.43	2.41	170.57
Entry	29	16.49**	8.25	0.027**	17.95	17.05**	466.55**
Group 1	7	10.43**	3.62	0.006	17.17	3.47	92.67
Group 2	6	3.52	10.78	0.009	16.84	1.44	98.19
Group 3	7	5.83	4.19	0.003	23.21	0.74	60.01
Group 4	6	31.54**	8.53	0.032**	14.94	24.43**	690.82**
Among groups	3	-	-	-	-	-	-
Error	58	3.26	5.92	0.006	14.03	1.55	51.55
CV (%)		18.35	27.59	9.04	119.26	4.29	14.77

**Indicates significance at the 1% level of probability.

Table A5. Analyses of variance for five traits measured on mass selected populations and their testcrosses grown at Martinsburg in 1978

Source of variation	d.f.	Mean squares				
		Root lodging	Stalk lodging	Ears/ plant	Dropped ears	Grain yield
Rep	2	3.17	1.19	0.003	31.00	55.16
Entry	29	9.74	9.09**	0.020**	5.17	221.10**
Group 1	7	8.89	2.94	0.008	7.15	31.93
Group 2	6	4.37	5.10	0.004	4.73	22.98
Group 3	7	22.11**	3.86	0.004	2.65	27.04
Group 4	6	2.13	20.86**	0.015*	6.42	320.80**
Among groups	3	-	-	-	-	-
Error	58	6.93	3.20	0.006	6.18	15.63
CV (%)		26.35	16.13	8.23	120.41	8.37

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Table A6. Analyses of variance for three traits measured on mass selected populations and their testcrosses grown at Nashua in 1979

Source of variation	d.f.	Mean squares		
		Ear height	Grain moisture	Grain yield
Rep	2	1415.22	67.79	173.41
Entry	29	338.96**	10.72	416.69**
Group 1	7	502.45**	8.24	48.39
Group 2	6	253.65**	8.20	35.95
Group 3	7	175.52*	8.13	29.25*
Group 4	6	370.63**	16.64*	700.06**
Among groups	3	-	-	-
Error	58	70.48	7.50	49.74
CV (%)		4.70	8.15	12.14

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Table A7. Analyses of variance for three traits measured on mass selected populations and their testcrosses grown at Ames Agronomy Research Center in 1979

Source of variation	d.f.	Mean squares		
		Ear height	Silk date	Grain yield
Rep	2	85.01	3.02	210.57
Entry	29	403.16**	25.28**	673.03**
Group 1	7	294.47**	5.71**	69.60
Group 2	6	106.97**	1.00	154.53**
Group 3	7	149.79**	2.52*	60.71
Group 4	6	851.68**	37.93**	781.91**
Among groups	3	-	-	-
Error	58	24.93	0.93	38.21
CV (%)		3.15	3.21	9.37

* and ** indicate significance at the 5 and 1% levels of probability, respectively.

Table A8. Analyses of variance for four traits measured on mass selected populations and their test-crosses grown at Ankeny in 1980

Source of variation	d.f.	Mean squares			
		Root lodging	Stalk lodging	Grain moisture	Grain yield
Rep	4	14.00	1.61	0.55	702.07
Entry	22	29.81**	2.25	3.01**	7774.72**
Group 1	7	9.43	1.64	1.68	85.17
Group 2	4	8.24	0.85	1.14	106.01
Group 3	6	10.20	1.83	1.88**	158.54
Group 4	2	112.62**	6.51**	17.45**	1489.88**
Among groups	3	-	-	-	-
Error	84	4.73	1.79	0.56	113.05
CV (%)		20.78	30.32	4.04	19.63

**Indicates significance at the 1% level of probability.

Table A9. Analyses of variance for four traits measured on mass selected populations and their testcrosses grown at Ames Agronomy Research Center in 1980

Source of variation	d.f.	Mean squares			
		Ear height	Ears/plant	Silk date	Grain yield
Rep	4	126.08	0.010	0.72	174.86
Entry	22	330.72**	0.019**	51.57**	986.68**
Group 1	7	279.77**	0.011	21.34**	181.23
Group 2	4	173.34**	0.002	4.46	101.52
Group 3	6	83.12*	0.011	4.77	167.13
Group 4	2	1345.40**	0.016	111.27**	1552.08*
Among groups	3	-	-	-	-
Error	84	34.39	0.009	2.71	98.47
CV (%)		4.15	10.49	7.01	16.24

* and ** indicate significance at the 5 and 1% levels of probability, respectively.